Systematic Zoology

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Systematic Zoology

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On the Nature of the Species

PAUL A. MEGLITSCH

IT IS a curious fact that the species, although the pivotal conception in systematic biology, has never been defined with precision in terms upon which the great majority of biologists have been willing to agree. To John Ray the species seemed somewhat more variable, somewhat less fixed, than to Linnaeus, and every generation of biologists since, to a greater or lesser degree, has aired its differences of opinion in our journals.

The original goal of the great systematists who initiated the classification of animals was to provide a system of hierarchical categories, based upon morphological similarities and differences, which would comprise a convenient catalogue of extant organisms. To these early workers the species appeared as a static and permanent group, for the concept of evolution was still to be developed. But the truth of evolution shone through the system of classification which they invented. Their work stimulated evolutionary speculation and later, when Lamarck, Darwin, and others had formulated tenable theories of descent, the systematists played a very active part in confirming the new concepts. In this process the systematist accepted a new labor—that of arranging his categories in such a way that they would reflect the actual course of evolution. As attempts were made to work fossil forms into the classificatory structure new problems arose, but the endeavour has persisted and a reasonably satisfactory scheme has been evolved. The fact is that the systematic structure envisioned by the earliest workers was admirably adapted to the new purpose in many ways and was from the outset arranged to a considerable extent along the lines of a natural classification. It was evident from the first that if there were, actually, an evolutionary process the species must be a temporary phenomenon rather than a fixed category, that new species must appear as old ones vanish or differentiate into several types. Darwin's choice of a title is sufficient evidence of the early appreciation of this fact. It was generally assumed, however, that the species changes on a time scale so vast that for all practical purposes it could be treated as if it were unchanging and permanent. In more recent years, however, the discovery of mutations and other kinds of enduring changes of the germ plasm, and to an even greater extent the establishment of the field of population genetics, provided an insight into evolutionary mechanics. It became evident that the species, along with all of the other categories of the natural classification, must take its place as a natural unit—as some particular point in the evolutionary process. Accordingly, new conceptions of the species began to appear in conflict with the traditional conceptions of the early systematists.

Past developments in the field of systematics and our discussions of the species category have tended to culminate in three more or less overlapping, more or less distinctive, conceptions of the species. Within these three schools of thought there are nuances of interpretation and minor areas of disagreement the discussion of which is beyond the scope of this paper. Let us content ourselves with examining some of the basic tenets of the three principal viewpoints with the idea of determining something of the potentialities and limitations of each, and with the hope of finding some common ground upon which all can meet.

It is not easy to choose among the many excellent statements of the various points of view. The particular ones which the writer has chosen seem to him to embody,

to a very marked degree, the fundamental viewpoint of the school which it represents in a particularly pure form. The so-called morphological school, perhaps better thought of as the phenotypic school, adheres to the viewpoint expressed by Gilmour (1940), who states that the "species is a group of individuals which, in the sum total of their attributes, resemble one another to a degree usually accepted as specific, the exact degree being ultimately determined by the more or less arbitrary judgement of taxonomists." The genetic viewpoint is admirably expressed by Dobzhansky (1936), who conceives of the species as that stage of the evolutionary process "at which the once actually or potentially interbreeding array of forms becomes separated in two or more separate arrays which are physiologically incapable of interbreeding." Huxley (1940) states the phylogenetic species concept in these words: "Species may be properly regarded as natural units, in that they are groups which a) have a geographical distribution-area; b) are self-perpetuating as groups; c) are morphologically (or in rare cases only physiologically) distinguishable from other related groups; and d) normally do not interbreed with related groups, in most cases showing partial or total infertility on crossing with them (though neither the lack of crossing or of fertility is universal)."

Each of these points of view is stated without much equivocation. To Gilmour the species is, as Linnaeus might well have maintained, a stage in the systematization of data rather than something which exists in nature. As a construct of the mind its nature will be determined to a very considerable degree by matters of convenience. To Dobzhansky, as to Huxley, the species is something which exists in nature, an entity to be sought out rather than created. To Dobzhansky the species is a natural unit which is continuous in the dimension of time and is integrated by the random flow of genes throughout the natural range of the organism as generations pass. To Huxley, also, the species is a natural unit, but not one which can be recognized by strict adherence to a single criterion. The delineation of the species may result from the biological forces which isolate one strain of germ plasm from another, by discontinuities resulting from geographical distribution, or by evidence of marked morphological or physiological differentiation, with the understanding that as a rule all will go hand in hand, while in occasional "difficult" cases one or another will become critical despite the failure of the other criteria to apply. It is implied that this lagging of differentiation in some respects is temporary, and one infers that eventually the distinctive stock will exhibit all of the characteristic types of species differentiation.

The Phenotypic Species Concept

It is important, at the outset of our evaluation of the phenotypic species concept, to remark that it is doubtful if anyone really believes in this idea, although there are many systematists who pay lip service to it. This fact shines through Gilmour's description of the phenotypic species as he speaks of "more or less" arbitrary judgements of the systematist. The proponents of the phenotypic species concept do not question the fact of evolution, nor that evolution is a statistical phenomenon, a phenomenon of populations rather than of individuals. The point of view which is maintained is that it is either impossible or impracticable to attempt to make the species group conform to the evolving population. This leaves the inference that a phenotypic classification is either possible or practicable, or, at any rate, is simpler to achieve.

Let us examine this supposed simplicity and, at the same time, note the ways in which the phenotypic systematist has tended to deny his avowed tenets. He need not have taken form as the most important single phenotypic attribute of organisms in working out a classification;

in nearly every group, however, classification has centered about the analysis of form. This is in part the result of biological history, for the form of organisms was studied long before precise studies of function were undertaken. Only where form has proved to be too simple to provide an adequate basis for classification and where culture is relatively easy, as in the case of some of the microscopic fungi, has physiological classification emerged. Form has retained its place at the focal point of classification even in modern times partly because of its many desirable features. It is relatively easy to quote differences of form by presenting exact measurements as well as by providing drawings and photographs. It is, by and large, easier and cheaper to collect data on form than on physiological processes, ecological behavior, or the other attributes which are directly or indirectly the phenotypic expression typical of a species. An even more desirable characteristic of form is its persistence after the death of the organism, for this makes a comparison of preserved specimens possible. On the whole the species as a phenotypic array is understood as a morphological type, although it is doubtful if any taxonomist, in describing his species, would be willing to ignore entirely an obvious physiological trait. Despite all of these desirable features, however, the analysis of form is neither straightforward nor simple.

To the earliest systematists form seemed a static rather than a dynamic property of organisms. The supposed fixity of the species was paralleled by a supposed fixity of form. Little attention was paid to the variability of the adult organisms, and when in later days it became apparent that variability was far too common to be ignored entirely, the systematist often attempted to avoid its analysis by designating a single specimen as a holotype.

Form, however, is not static and cannot be understood on that assumption. Its careful analysis requires the most delicate attention to the details of its constant change. Form is more than the mere spatial arrangement of the component parts of an organism; it is a momentary aspect of the continual interplay of the action and reaction between matter and energy; it is an event in space-time. As a result form is a plastic attribute of organisms, constantly changing in response to external and internal stimuli, and, like wheels within wheels, changing at diverse tempos and through diverse cycles. The salinity or acidity of a pond, its temperature and the amount of light which strikes its surface, all affect the form as well as the behavior of its inhabitants. In many instances samples of organisms originally thought to be distinct species have been found to represent mere morphological variants of the same species, variants evoked by the interplay of environmental and internal factors upon the genic complex of a single species (see Schröder, 1914, for example). Even in a constant environment the larval animal becomes an adult only by undergoing a series of morphological and physiological transformations of the most profound nature. In a number of cases immature organisms have been classified in different phyla from their corresponding adults until the riddle of their relationship was solved. Physiological cycles, such as those accompanying the internal stimuli associated with the changing seasons, may evoke such extensive adornment of one or the other sex that the different phases appear to the uninitiated to represent different species. Meanwhile, and more obscurely, the often nearly imperceptible morphological consequences of the evolutionary process take shape about us. With all of its advantages form is not a simple attribute for the systematist to analyze, and nearly every factor associated with the dynamics of form has, at one time or another, in one group or another, caused serious systematic difficulties. The simplicity of the phenotypic species concept is thus found to be largely illusory.

It is illusory, however, only because we are unwilling actually to build a classification based upon form alone. If we grant every kind of morphological difference equal value, there is no problem in the analysis of form. The fact is that the classical systematists while believing themselves adherents of a morphological species concept were responsible for untangling most of the puzzling problems in the analysis of form mentioned above, and by so doing were denying that a species is a morphological type and nothing more. They recognized immediately that every distinct morphological type is not a distinct species. Male and female, however greatly they differ, must belong to the same species if they always interbreed, as must larva and adult, winter and summer phase, brackish and freshwater variant. No one today would seriously propose that all of these differences be granted equal value in a systematic scheme. Why? The fact is that the classical systematists developed a system of classification upon the phenotypic, and especially upon the morphological, attributes, but while so doing they comprehended the species as an assemblage which is linked together genetically in some way or another. It was generally understood that except, perhaps, in cases of interspecific hybrids, all the offspring of two parents, regardless of their developmental stage or the morphological differences that the accidents of existence imposed upon them, should belong to the same species group. The modern systematist, therefore, has not introduced a radically new element into the philosophy of systematics in his attempts to describe more accurately the nature of the genetic link between the various individuals belonging to a single species.

It is this fact that leads Gilmour to speak of "more or less" arbitrary decisions, for once it is understood that some genetic link is implied by the term species the inference is clear that while the systematist may be arbitrary the species is not. One may, on epistemological grounds, doubt that the systematist has been able to escape the arbitrary, but the fact remains that one cannot be truly arbitrary about his descriptions of the real. The description may be good or poor, may be adequate or inadequate; it may embody all of the data necessary to characterize all organisms and only organisms which possess this genetic link in common, or it may fail to do so. In either case it is not a matter of arbitrariness, nor of taste, nor yet of convenience. A natural classification can be based only upon a species which is a natural unit.

Adherents of the phenotypic viewpoint may stress the idea that a natural classification is either unworkable or impossible. Thus Gilmour (1940, p. 469) remarks: "From the philosophical point of view a natural group is . . . no more real than an artificial one; both are conceptions built upon experience alone." Throughout his discussion, Gilmour emphasizes the epistemological problem of the scientist. He observes that the scientist must depend upon sense data, and in order to recognize any single object there must be a correlation of the sense data he receives. Gilmour points out that the scientist does not face this problem squarely. To the writer it seems that it is not necessary that he do so in the practical everyday business of his research. As an avenue leading toward a comprehension of the limitations and potentialities of science, and as a reminder of the basic assumptions upon which all science rests, epistemological thought is of prime importance. Nevertheless all science is wrought of just such conceptions based upon experience alone, and the scientist assumes that the manipulation of sense data according to certain patterns will produce and has produced a series of useful approximations. If this basic assumption is false, all of science falls together. If it is true, and to the extent that it is true, science acquires a certain validity as a part of the fabric of knowledge.

Considerations such as these cannot es-

tablish the fact that science, or any of its branches, must of necessity be arbitrary. Within the limits of each scientific discipline we apply our techniques to the best of our ability with the objective of describing the real world. Of our results, incomplete and fragmentary perhaps and often misleading, we can be justly proud. The one reason above all, it seems to the writer, has been that the scientist has tried not to define things. One defines an abstraction with precision, but one cannot define a thing. One describes a thing, constantly adjusting one's viewpoint as one learns more about it, fitting the conception to the object rather than assigning the object to some preconceived pigeonhole. If the species were something to be defined arbitrarily there could be no real argument about the nature of the species. One might wish to argue about the most convenient size of pigeonholes, but there would be no possible answer that would fit all cases, and no tendency to believe that there were important conceptual aspects to the discussion.

It has also been maintained that the oldest goal of the systematic biologist, that of providing a useful catalogue of organic diversity, will not be served if we permit the species concept to become something other than a phenotypic one. In a sense this argument can have little weight, inasmuch as we have noted that phenotypic differences, in the absence of a genetic link, have not been utilized for species description. Nevertheless, it may be well to observe that the catalogue, for and of itself, is of little value unless it represents something that is real in nature, or, alternatively, unless it can be used in the establishment of sound operational definitions for experimental biologists.

The importance of sound operational definitions is very great. Science has been defined as an attempt to systematize our knowledge of the circumstances under which recognitions take place (Whitehead). It is only as we learn to describe the conditions which obtain in an experiment or observation and the materials with which we work that we can achieve dependable operational definitions. Upon the precision of these definitions the reproducibility of our data depends. In this area the physical scientists have been able to develop a more precise terminology than the biologists, for many of their terms approach the ideal of the single-valued term. Sodium chloride, for example, is understood to mean the same thing by all who use the term. Even in the absence of perfectly pure preparations the relative precision of their terms is an instrument in their hands facilitating the relative precision of their operational definitions. *Paramecium aurelia,* on the other hand, is a multivalued term, as the work of Sonneborn and his students have so clearly shown. As a result, the experimental worker who deals with *Paramecium aurelia* has in the past failed to define sufficiently the materials with which he experimented. We may never, in biology, achieve the precision of the physical scientists because of the phenomenon of individual variability, but nevertheless, as we bring our species category closer to the goal of a single-valued term we bring a greater precision to our operational definitions and a greater reproducibility to our data.

It is not enough for the experimentalist to know that the left anal cirrus of a hypotrich is 10 per cent longer than the next in line. What he does need to know is that any organism having this trait belongs to a relatively coherent population, the variability of which falls within certain definite limits whenever and wherever the material is obtained. This goal can be achieved only when the species group corresponds to some real entity in nature; and it is clearly incumbent upon the systematist, as a cataloguer or as a scientist is his own right, to find ways of making the species group conform to a natural unit of some kind.

The Genetic Species Concept

Dobzhansky has suggested that the species be defined as an interbreeding population, physiologically incapable of interbreeding with other more or less similar populations. Ideally, such a population would appear to have a particular kind of objective reality. It represents a discrete adaptive peak in the field of gene combinations which maintains its integrity as the result of interbreeding. Such a population will, indeed, act as a unit in the evolutionary process, as it will also in the community in which it lives. Dobzhansky's concept appears to be very tidy, as it sets up but a single criterion for the decision as to the distinctiveness of a population.

It has been said that this conception of a species, useful and tidy as it may appear in theory, is unworkable. With the use of this criterion alone, only living organisms can be recognized, and the museum worker would find himself in serious difficulties. While the observations needed to demonstrate the ability or inability of two groups to interbreed could often be made in the field, laboratory work could be restricted to those organisms which could be kept and bred successfully in captivity. Furthermore, as Marston Bates (1950) has it: "Sometimes animals that wouldn't touch each other with a ten foot pole in the wild carry on scandalously if they are put in a cage together. Other animals that have no inhibitions in the woods take monastic vows as soon as they are put in a cage."

One species does not become two in an instant; there is a period of differentiation, and the exact moment when an incipient species deserves rank as a true species must be chosen arbitrarily no matter what criteria may be set up to define this point. As Arkell and Moy-Thomas have put it (1940, p. 396), "the question 'what constitutes a species?', always so troublesome to the neontologist, hardly concerns the paleontologist, since the more he learns of phylogeny the more arbitrary must be the distinctions he draws between his species." This enforced arbitrariness, so clear to the paleontologist who sees his species distributed in the dimension of time, may be less evident to the systematist who deals with extant organisms. Actually the problem is the same; the differentiation of the species clusters undoubtedly takes place in the same manner. What shall we do with populations which are but partially isolated? It will be necessary to determine the degree of infertility which they show and the quantity of gene flow between them, and to calculate the amount of interbreeding that can be accepted without materially influencing the evolutionary changes of the two populations.

To the writer it would appear that the objections mentioned above are not particularly weighty ones. We shall, of course, find it necessary to speak of incipient species populations in some groups, populations which have not yet acquired the status of a true species. We shall need, also, to follow the established techniques of the geneticist, to learn to recognize the genes common to members of a species by observing the attributes with which they are associated. It is not necessary to show that a whale and a hippopotamus will not mate. We can see their distinctiveness by the phenotypic attributes which they exhibit. The systematist accepting Dobzhansky's definition of the species merely accepts a new description, and a more precise one, of the genetic link which exists between the members of a species group. He will, accordingly, search for attributes which successfully delineate the genetically discrete populations. Where he succeeds his species will be valid. Where he fails they will be invalid, and some later worker may correct the error. Science does not deal with absolute truth, but with useful approximations. The systematist, therefore, can only be expected to produce descriptions which approximate the natural group.

There are other difficulties associated with an unqualified acceptance of the ge-

netic species concept, difficulties which Dobzhansky has seen as clearly as anyone else. While there can be little doubt that in the great majority of cases the adaptive peak coincides with the reproductively isolated population, there are cases in which exceptional situations prevail. Dobzhansky mentions a number of these, some of them fairly well known. Hybridization between apparently well-differentiated populations is common in some groups, notably among plants, but also among fishes and a few other kinds of animals. Partially isolated populations, from the reproductive point of view, are not too uncommon among geographically isolated forms. Species complexes, such as those occurring among the gall wasps and studied extensively by Kinsey and Goldschmidt among others, present another exception in which lines of intergrading and interbreeding species are found looping back, in some cases, to the same region and the same host several times and exhibiting complete reproductive isolation at remote points of the species chain. Gene spread follows along the whole chain, thus in theory eventually extending to all parts of the whole complex. In such cases we are not dealing with an isolated adaptive peak but with an integrated adaptive range composed of a number of indistinct peaks. It is evident that there is a lack of universality among organisms with respect to the correspondence of the reproductively isolated unit and the limits of the adaptive peaks.

We are sometimes tempted to force reality to assume a false conformity with our conceptions. The genetic species concept is helpful, for it calls attention to one very important attribute of the adaptive peak as it exists among a large number of organisms. We must not, however, permit the concept to dominate the reality which subtends it. If the species is truly an objective unit we cannot define it; we can but describe it. Insofar as our species concept is to be a tool facilitating the description of reality it will be an inductive generalization itself, not an *a priori* conception. The genetic species concept is not wholly invalid, nor wholly arbitrary, nor, for that matter, wholly an *a priori* abstraction. Nevertheless it fails to apply to all kinds of organisms, and, in this sense, is incomplete.

The most unfortunate limitation of the genetic species concept is its inapplicability to groups in which biparental reproduction does not occur. Dobzhansky (1936, p. 319) says: "The modification of the evolutionary patterns wrought by the obligatory asexual reproduction and self-fertilization manifests itself in the absence of a definite species category in such organisms." Later he amplifies this point of view. "The above statement should not be misunderstood as implying that variation in asexually reproducing species is absolutely continuous. On the contrary we find there aggregations of numerous more or less clearly distinct biotypes, each of which is constant and reproduces its like if left to breed. These constant biotypes are sometimes called elementary species, but they are not united into integrated groups that are known as species in the cross-fertilizing forms." He points out that the asexual biotypes, like the sexual species, are clustered about adaptive peaks in the field of gene combinations, while adaptive valleys remain more or less uninhabited, and that these clusters are arranged in an hierarchical manner. This leads to the conclusion that "different clusters, then, may be designated, some as species, others as sub-genera, still others as genera, etc. Which one of these ranks is ascribed to a given cluster is, however, decided by considerations of convenience, and the decision is in this sense purely arbitrary. In other words, the species as a category which is more fixed, and therefore less arbitrary, than the rest is lacking in asexual and obligatorily self-fertilizing organisms. All of the criteria of species distinction utterly break down in such forms."

Du Reitz (1930) suggested that we dis-

tinguish between asexual and sexual species. This choice of terms is somewhat unfortunate, since obligatorily uniparental sexual behavior is not uncommon among some groups of organisms, and these, too, will lack the integrative forces stemming from interbreeding. It would appear, therefore, that the terms uniparental and biparental species are preferable.

Dobzhansky was aware that the restriction of the term species to biparental organisms alone would be a more or less unpopular move. He remarks: "The binomial system of nomenclature, which is applied universally to all living things, has forced systematists to describe 'species' in the sexual as well as the asexual organisms. Two centuries have rooted this habit so firmly that any thorough reform will meet with a determined opposition. Nevertheless, systematists themselves have come to the conclusion that sexual species and 'asexual species' must be distinguished. In the opinion of the writer, all that is saved by this method is the word 'species.' "

If there were any real evidence that there is some difference between the kinds of adaptive peaks in sexual and asexual organisms it would seem that Dobzhansky's point is well taken. Actually this does not appear to be the case. Among Protozoa, for example, we sometimes find species belonging to the same genus differing with respect to the occurrence of biparental reproduction. In the case of *Paramecium aurelia*, for example, we are dealing with a system of eight known physiological species which are reproductively isolated, of which seven are biparental while one is uniparental (see Sonneborn, 1948). In the opinion of the writer much more is salvaged than the word species if we apply it to all organisms, uniparental or biparental; we save a term which conveys the area of similarity which all natural populations exhibit, whatever this may be, resulting in a common evolutionary impulse. The species is to the complex fabric of evolutionary change what a cell is to a multicellular organism.

The Phylogenetic Species Concept

Huxley's definition or, rather, description of the species group begins with the idea of the species as a natural population and offers several attributes of such populations as criteria for their recognition. It is, in a sense, a synthesis of the older viewpoint of the species as a phenotypic assemblage and of the population as an evolving unit in the modern sense. It recognizes the fact that the species assemblage is to be characterized on the basis of its appearance and physiology, but emphasizes that these traits are the means by which we attain an end—the recognition of distinctive populations. It fits admirably into that intermediate territory between the views of the phenotypic school and those of the genetic school.

The principal objection to the ideas expressed by Huxley is that there is no single criterion upon which the species can be recognized. His view lacks, therefore, the superficial tidiness of either of the other two schools. Nevertheless this apparent weakness is, in many respects, its strongest point. The fact is that the evolutionary process which we attempt to study and understand, and the effects of which we attempt to express in our classificatory system, does not embody a single kind of differentiation nor does it come about through the agency of a single set of forces. Evolutionary differentiation includes the diversification of stocks with respect to morphological, physiological, and ecological attributes and also includes the differentiation of isolating mechanisms which eventually result in a failure of interbreeding. While these processes may, and no doubt usually do, occur in ways which are essentially similar, the fact remains that this differentiation of the soma is independent of the differentiation of the germ plasm to a very great extent. As a result there are really two independent processes going on, often, no

doubt, at different rates. Where the rate of somatic differentiation outruns that of germ plasm differentiation, complexes of interbreeding groups which are phenotypically distinct will arise. A classification which is capable of providing a sound basis for establishing operational definitions must recognize and include this type of differentiation. Where the rate of somatic differentiation is lower than that of differentiation of germ plasm, we shall find closely related, similar populations, reproductively isolated but otherwise very much alike. We would find the complex of physiological species of *Paramecium aurelia* in this category. Despite their morphological similarities, however, physiological differences of some kind will no doubt characterize most such species. Certainly sound operational definitions will require that these be accorded specific status. With Huxley's description of the species all of the major types of diversification are given a place. Insofar as we are capable of using the battery of criteria as an aid in recognizing a natural population rather than as a measuring stick for determining whether a term which has been defined *a priori* shall apply, we shall be in possession of a relatively mature species concept, empirical in flavor, the result of inductive generalization rather than of deductive speculation.

Despite its apparent advantages, however, this concept of the species cannot be meaningful if, as Dobzhansky implies, there is no real population, in the evolutionary sense, where interbreeding does not occur. For an examination of this problem uniparental organisms appear to represent critical material.

The Evolving Population in Uniparental Organisms

It would be difficult to convince anyone who has spent much time in the systematic study of uniparental organisms that there is no evolving population represented among them. The writer has devoted considerable time to the study of Myxosporidia, which appear to be obligatorily uniparental, reproducing sexually by autogamy. Among Myxosporidia, as among other uniparental organisms, biotypes remain constant despite the lack of interbreeding. Surprisingly variable traits remain unchanged in a population despite the fact that there is no recombination of genes. *Ceratomyxa truncata,* for example, has spores which are bivalved, trivalved, and tetravalved. It was originally discovered in 1895 by Thelohan, and recovered in 1912 by Parisi, a span of years representing many Myxosporidian generations. We are so familiar with such biotypes that it is difficult to avoid forming the point of view that it is not that the uniparental organism lacks a species assemblage, but rather that we have not succeeded in describing the peculiarities of the assemblage with sufficient care. Nevertheless, if we are to include the biparental and uniparental species in the same classificatory system, as parallel categories, it must be as essentially similar groups, and perforce, as natural groups. Is there any way to regard the uniparental population as an evolving population? Does the biparental population have a fundamental similarity with the uniparental population at some level of magnitude?

We are sufficiently familiar with the picture of an evolving population as an aggregate of similar organisms, occupying a more or less continuous habitat, and more or less discontinuous from all similar forms as a reproducing unit. Within this assemblage of organisms intragroup competition and cooperation occur in the business of daily living. Competition is more or less keen, depending upon the reproductive potential of the organism and the degree to which the ecological niche that it occupies has been exploited, while cooperation may be more or less effective depending upon the concentration of the organism within its spatial range. Extragroup relationships also provide competitive and cooperative factors in the complex of forces affecting the population.

The significance of the competitive factors depends upon the number and size of other populations which have similar requirements and occupy, at least in part, the same habitat, while the degree of cooperation depends upon the nature of the organisms involved and their relative abundance. All of these factors contribute materially to the nature and strength of the selective forces which act upon the population and thereby affect the direction and tempo of the evolutionary process. Internal physiological interrelationships are also concerned with the development of selective pressures, for a harmonious gene complex and a harmonious phenotypic physiology is required for the maintenance of a successful organism. Change in the population occurs as the result of differential survival and differential net reproductive rates, fixed into permanency by net changes in the gene frequencies which exist in the hereditary pool resulting from these forces. The tolerance of the germ plasm for interbreeding with other forms is an important factor in determining the speed with which reproductive isolation will be achieved and the extent of isolation which will be maintained in the future. In some cases, at least, hybridization may provide a method of producing new species, although in most groups these cases will be relatively rare. Hybridization itself may create selective pressures, particularly where it results in infertile, or relatively infertile, young, for loss of gametes by hybridization will tend to favor the establishment of types of gametes which are impervious to the gametes of other species. The flow of genes throughout the interbreeding group, as generations pass, serves to integrate the population, and assures that it will reproduce as a unit and evolve as a unit. Among uniparental populations no such integrating force exists, and whatever stability the adaptive peak may possess must stem from other sources.

Only the germ plasm of the population enters directly into the evolutionary process. The soma, as a temporary product of the germ plasm, influences its evolution only as its attributes are associated with differential survival or differential fertility. While elements other than nuclear genes may enter into the control of attributes, our evidence favors the viewpoint that they are the most important single kind of factor, and we may think of the various gene constellations represented in the various germ plasm lines of the population as the basic materials upon which the evolutionary process acts. At any given moment each allele is found in a certain percentage of the extant gene constellations. Through differential survival and differential breeding rates the percentages come to shift, and with this shifting the attributes of the population as a whole change. Evolution may be understood as changes in gene frequencies exhibited by a population under the influence of survival, breeding, and mutation rates.

With each generation there is a reshuffling of the alleles, resulting in the production of new zygotic configurations. Competition for survival begins immediately, for as Timofeef-Ressovsky (1940), for example, has shown, the relative viabilities of the ova may be influenced by gene harmonies. The zygotic gene constellation subtends the production of the individual, controlling many of its attributes, and it is natural to think of the gene constellation as being the more basic conception. But in the dimension of time, zygotic gene constellations are no more permanent than the individual itself. Both are temporary phenomena, arrangements which exist for only a generation, mere swirls in the current of genes flowing along the stream of time. The essential elements of the population are the hereditary factors themselves, for these, directly and persistently, produce their like or mutate to allelomorphic forms which in turn produce their own kind, or, in some instances, disappear or are modified by chromosomal aberrations. In the ultimate analysis the biparental population is the visible

consequence, under a given set of environmental conditions, of an evolving, changing, recombining, reproducing, and "dying" population of genes, the members of which are constantly changing in relative frequency and being rearranged in new but temporary patterns.

Although the patterns characteristic of the reshuffling process necessarily vary with the reproductive behavior of organisms, all sexually reproducing species, whether biparental or uniparental, will exhibit a rearrangement of gene constellations with each meiosis and syngamy. It has been customary to assume that uniparental sexual organisms must eventually become homozygous, or very nearly so. Considering the reproductive process in the complete absence of selection or mutation this is more or less inevitable. There are some indications, however, that a selection against homozygosity may sometimes occur. The phenomenon of hybrid vigor, for example, has been explained on the assumption that increased heterozygosity has a stimulating effect, in addition to the possible positive contributions of both allelomorphic factors upon traits other than those with which they are usually associated. Furthermore, if, as Wright (1940) suggests, the majority of mutant genes are inferior to the wild type, a mechanism exists which would tend to preserve a certain degree of heterozygosity in selfing organisms. In *Paramecium aurelia,* on the other hand, the individual undergoing autogamy produces homozygous strains. It is not clear whether this type of behavior is widespread among ciliates; the writer is inclined to think that, in general, as homozygosity increases in a population, it may be associated with reduced vitality until, at some point, a selection in favor of heterozygosity will come into operation even in uniparental forms. This would tend to provide a limited reshuffling of alleles with each uniparental generation, similar in type, but not in extent, with that occurring in the genic pool of biparental forms. This reshuffling is limited to the confines of the progeny of a particular individual, and in no way provides for gene spread from one clone to another. Whether or not it is of any great importance to the uniparental population, then, it cannot be seen as an integrating force comparable with that exerted by gene spread resulting from interbreeding.

It is essential that we distinguish between the end and the means. Among biparental forms a genic pool exists because of the common ancestry of existing members of the species. In an adaptive peak of uniparental organisms a population of genes exists in which the currents and swirls are different, to be sure, from those occurring in the biparental gene pool, but which nevertheless contain similar genes because of the descent of extant organisms from common ancestral stocks. Although the mechanisms by which reproduction is effected may be different in the two cases, the end result remains the same. Among biparental species the unity of the gene pool is maintained in part by the integrating action of interbreeding, and in part as the result of selection favoring certain alleles and certain combinations of alleles. Among uniparental species the constancy of the population of genes is maintained only as a result of selective forces. Both kinds of populations, if small, may be materially altered by the chance survival of offspring not better adapted than others which have happened to die. Nevertheless, in both populations, biparental and uniparental, the operation of somewhat different factors results in a population of genes which has a certain degree of stability, and, while the means may differ, the end result is the same.

It has been more or less customary to assume that one of the factors tending to stabilize and unify the population of genes in biparental organisms is of more importance than the other, to emphasize the cohesive effect of interbreeding. But it has not been clearly shown that this force is stronger than selective forces favoring the status quo. Any continued selection favoring the continued existence of alleles now

predominant, of gene constellations now common, will tend to preserve the identity of a species assemblage and to discourage proliferation of variant types. The strength of this stabilizing, centripetal selection is at present undetermined, but there are some indications that these forces may be significant. The generalization that mutant genes are or tend to be inferior to the wild type is one such indication. The work of Timofeef-Ressovsky (1940) also suggests that a considerable selective pressure stemming from the requirement for harmonious combinations of genes within the zygotic constellation exists, even during early development.

Centripetal selective forces, if of sufficient strength, would tend to maintain a certain degree of uniformity among the members of a species group, even though a considerable period of isolation had elapsed. The strength of such centripetal selection would tend to reveal itself in the degree of uniformity among individual members of a population, and by the similarity among populations which have not been allowed to interbreed for some time. The subtlety of the interrelationships which must exist within the organism and between the organism and its environment is very considerable. The student of morphology and of physiology is continually struck by the constancy with which certain gross features, major elements of the organizational plan of the organism, are correlated. The constancy of these correlations provides the basis for the science of anatomy and of comparative physiology. If we have some information about a few of the systems of an organism we can predict, with considerable accuracy, the basic features, but not the details, of other systems. These constant relationships are not the product of chance alone. They are, in fact, present despite the element of chance as it manifests itself in random mutation. They exist because a certain harmonious relationship of parts is required for survival. In a similar way, we discover that if we understand a portion of the ecological community in an area we can predict, with some accuracy, the general nature of some of the more important remaining organisms. Ecological as well as physiological interrelationships must be harmonious. Predictability presupposes the operation of underlying principles, whether or not they are clearly understood, and in these areas it appears that the principles may well be those which subtend the harmonies between part and part or between organism and organism.

In some groups isolation is followed by a rapid and marked differentiation of morphological or other characters, while in other groups differentiation appears to be slow. It may be supposed that in those organisms in which the harmonious relationships, internal and external, are very delicately balanced centripetal selection will be strong, tending to prevent the differentiation of physiological, morphological, or ecological types. This may explain the existence of such systems of reproductively isolated strains (or species) as those found in *Paramecium aurelia*. There are eight physiological species, each effectively isolated from the others. It is not known how long these types have existed, but they (or at least some) are widely distributed, and it may be inferred that they are not extremely recent. The isolation of these eight types has not been accompanied by a degree of differentiation which is ordinarily recognized as representing phenotypically distinct species. It is remarkable that collections from North and South America, from Europe and Asia, should all fit into a total of eight physiological species. It is no less remarkable that the same physiological species should be recovered from Japan, from the United States, and from Scotland. One may be inclined to ask how many paramecium generations have existed since the last case of gene exchange between some of the more remote populations. Does this system support the idea that gene spread by interbreeding is a more powerful stabilizing influence than centripetal selection for the maintenance of

the species? If we assume that there is a considerable amount of interbreeding between the apparently isolated stocks of the same physiological species, we shall be hard put to explain the existence of innumerable local strains belonging to the same physiological species. On the other hand, if we accept the idea that there are no more than occasional exchanges of genes between adjacent populations, and very rare exchanges between populations living some distance apart, we are more or less forced to explain the maintenance of the basic attributes of the physiological species upon gene survival rather than upon gene spread. The marked differences in environment which the various strains of *Paramecium aurelia* must encounter in their diverse localities lead one to suppose that the major contribution toward stability of the physiological species from centripetal selection, whether it be a strong force or a weak one, has to do with intra-organismal harmonies more than with environmental ones.

Evolutionary change is wrought despite the conservative factors tending to prevent change. One of the conservative factors, of course, is gene spread resulting from interbreeding, a factor lacking in uniparental organisms. In uniparental and biparental organisms, however, centripetal selection will remain a stabilizing force. A bundle of sheaves tied together with two strings need be no more secure than one tied with a single string, particularly if the two strings be unequally tight. It seems to the writer that until more is known of the relative importance of centripetal selection as a stabilizing force it is not safe to assume that the uniparental population is less well integrated than the biparental population in the evolutionary sense.

Gene spread and interbreeding may be a creative force as well as a conservative force in the evolutionary process, for recessive mutant genes may be masked for a time, occasionally emerging for testing. Such genes may eventually happen to fall in with other genes which help to give them adaptive value. In the long run this may more than compensate for the inevitable slowness with which a recessive mutation can come to represent the predominant allele in an interbreeding population. The rate of change will be greater among the uniparental organisms in the sense that a recessive mutant gene will be constantly segregated out in one-fourth of the offspring of a selfing heterozygote or may express itself immediately in the offspring of a haploid (?) asexual organism. The rate of change will be slower in the uniparental organisms, however, in the sense that the mutant gene can survive only if the alleles necessary to form a harmonious complex with it are present in the parental genotype. It is, therefore, impossible for the uniparental population to exploit fully the creative possibilities of a mutant gene because of the restricted number of combinations open to it.

Once a mutant stock arises in a uniparental population, can it at once be considered a new species? The strain exhibiting the new trait is forever after reproductively isolated from the parental stock. This, however, is of little import, as the various members of the original population are also reproductively isolated from their own contemporaries just as effectively. Must we, with Dobzhansky, conclude that no matter how constant a uniparental biotype, no matter how suggestive their hierarchical arrangement, there can be no objectively chosen criteria for establishing one as a species, another as a subspecies, and still another as a genus?

The fact is that we have seen that the biparental population is considered an objective unit in the evolutionary process because of the possibility of gene spread carrying a new trait to all parts of the population's habitat. The statement is frequently made that biparental patterns of inheritance facilitate this gene spread. Actually this is not so, except that it may favor the survival of specific alleles by providing a greater variety of combinations in which they can seek for harmoni-

ous configurations with other genes. In a population which is essentially static in size, gene spread is effected only by differential survival of the alleles involved, and all instances of gene spread may be visualized as instances of gene replacement. Replacement of existing alleles by a new allele takes place among uniparental as well as biparental populations, and through the same agency—differential survival.

Let us consider the possibilities open to a mutant stock in a uniparental population. Once the mutant stock is established it can enter into a number of different relationships with the parent stock. It may be unable to maintain itself, and so will eventually disappear. No new species has arisen. Exactly the same thing may happen in a biparental population, although the alleles responsible for the distinctiveness of the mutant strain may be retained, if recessive, and occasionally reappear. The mutant stock may have an adaptive gene complex which will make it possible, eventually, to crowd out the original type. In this case the species may be said to have changed, but it is not necessary to speak of the formation of a new species. Exactly the same thing may occur in a biparental population, although it will tend to occur more slowly. The mutant stock may be altered so little that it remains in exactly the same habitat, retaining the same requirements of that habitat, and so competes, without advantage, with the parental strain. Exactly the same thing may occur among biparental populations. Assuming that the two populations are reproductively isolated, they may or may not be recognized as new species, depending on whether we happen to discover that a certain part of the population refuses to breed with another part, and whether we conceive of a species as necessarily distinguished by reproductive behavior alone. In the ecological sense, all of the members of both strains are related by intragroup competition, and there is but one species. Among uniparental organisms it would certainly be preferable to consider two such strains as identical, unless they were marked by very obvious physiological or morphological differences, a situation which is practically excluded by the type of relationship under discussion. On the other hand the mutant stock may be altered in such a way that it can no longer occupy the whole range of the parental type, although it competes, without real advantage, in a part of the distribution area. It would seem logical, under these circumstances, to consider the mutant stock as a geographical variant of the species. The mutant stock may, on the other hand, be altered in such a way that it cannot occupy a portion of the parental habitat but can occupy an area which is not satisfactory for the parental strain. Among uniparental organisms two such strains are evolutionarily distinct, for without the interference of some outside agency it will not be possible for either one to replace the other completely. In short, gene replacement by differential survival can occur, among uniparental organisms, only where the two strains occupy a single range, or where the range of one strain is a relatively larger area which completely encloses the range of the other strain. Among biparental organisms, two strains occupying ranges which overlap, but in which each strain has a portion of its range which is not shared, may or may not represent distinct species, depending upon whether there is sufficient gene exchange between the two strains in the common part of their habitat. The important point is that a species may be recognized objectively on this basis, whether uniparental or biparental, and that the basis upon which the recognition is made is evolutionarily significant.

The writer, then, would recommend that among all organisms, uniparental or biparental, the species be recognized as an evolving population which is distinct from other evolving populations. The study of genetics or reproductive behavior alone, of morphology or physiology alone, or of

ecology alone will not suffice to define such a population. Judgements should be made on the basis of accumulated information of all kinds. While in most instances, no doubt, morphological or physiological peculiarities will suffice to enable one to recognize different strains, or, at least, to characterize them once they are recognized, a careful analysis of the relationships of the population to its physical and biotic environment may be needed in some cases in order properly to delineate the evolving population. In the ultimate analysis, the evolving population emerges as a group of individuals, the genes of which may potentially spread over the same area, or at least, over areas which are not mutually exclusive, and which have such similar requirements of their environment that they are related by intragroup types of competition and cooperation.

It is the cohesive forces resulting from intragroup types of competition which tend to preserve the identity of the population among uniparental organisms, and which aid and abet the gene flow consequent upon interbreeding among biparental organisms. Once these cohesive forces have been ruptured, the recognition of a new species is indicated. For example, in the Myxosporidia, which have an autogamous life cycle (see Kudo, 1945, and Noble, 1940) and live as parasites of aquatic hosts, the parasites appear to occupy a discontinuous environment, for each lives only within the confines of acceptable tissues of an acceptable host. Inasmuch as the hosts are aquatic and in many instances occupy freshwater streams and ponds, the hosts themselves occupy a discontinuous environment. The spore stage, however, is more or less resistant and may, perhaps, be scattered over an area which extends well beyond the limits of the geographical range of the vegetative parasite. By this means the parasite may bridge the gap between potential hosts in the same stream or pond, or the gap between land-locked populations of host animals. The geographic distribution area of the myxosporidian is determined by (1) the ability of the vegetative organisms to inhabit one or several host species, and (2) the area over which the spores can be disseminated. A mutant strain can escape from the confining influences to which the parent strain is exposed by developing an ability to survive in some new geographical area through changes in its temperature requirements, or requirements in salinity, oxygen, etc., or by adapting to life in a new host species or host organ. In this new environment selective pressures will tend to be somewhat different and so hasten the differentiation of the mutant strain. When the environment of the parent strain has come to include space, hosts, or organs which are not available to the mutant strain, and at the same time the mutant strain has come to occupy a portion of the environment which is not available to the parental strain, we may conclude that the cohesive forces which have in the past been responsible for the maintenance of distinctiveness have been ruptured. Where the requirements of two strains are very nearly the same, so that there is a keen competition between them in the region of common occupancy, there will be a strong tendency for them to withdraw eventually from competition.

As the center of each population tends to shift toward the unique habitat which it occupies, a tendency toward allopatric distribution will, of course, result. Where a sympatric distribution exists, several entirely different points of view may be taken. One may suppose that the requirements of the two strains are so similar that they must occupy the same area. In such an instance sympatric distribution is evidence of close relationship. On the other hand one may suppose that the requirements of the two strains must be sufficiently different to permit them to occupy the same territory without excessive competition. In such a case sympatric distribution is evidence of divergence. It is

obvious that the two strains, if they possess identical requirements, must inhabit the same territory, unless accidental events result in a high incidence of one strain in a particular part of that territory. It is equally obvious that the extent to which they will compete depends entirely upon the population pressure existing at the time. Where there is a very dense population one may expect keen competition, whereas there may be very little competition when the population is sparse. It is probable that among the Myxosporidia, at least, population pressures are never very strong, for situations in which every host organism is infested are rare. The problem of transmission from one host to another is unquestionably more of a factor in the limitation of populations than competition between individual parasites for a place to live, at least in the great majority of cases. Where two strains are found inhabiting identical ranges, competing for the same host organ of the same species, it is evident that in the absence of some very obvious physiological or morphological trait, one must consider them as belonging to the same species, for it is evident that in the sense that alleles are capable of replacing one another throughout the population in case some new adaptive configuration develops, the two strains are reproducing as a unit.

The Species

The species, in the case of uniparental and biparental organisms, may be visualized as a natural population, evolving as a unit in actuality, or retaining the capacity to evolve as a unit if artificial barriers are removed. The integrity of the species depends upon gene spread resulting from interbreeding, gene spread resulting from differential survival in a field of free competition, and from the effects of centripetal selection, or from a combination of these factors. The species population is the visible manifestation of a pool of genes which retains its character as a unified pool because, in theory, any allele present may eventually come to replace all of the allelomorphic factors in the pool, either as the result of interbreeding, or as a consequence of simple differential survival in the case of uniparental organisms. This will require that the species population occupy a definite geographical (and biological, in the case of parasites) distribution area, to permit gene replacement. It will also be characteristic of species, in general, to exhibit morphological, physiological, and ecological peculiarities which are the phenotypic expression of the unique hereditary configurations present in the gene pool. A species, thus, is an independent and distinctive region of gene spread, regardless of the mechanisms involved in the distribution of these genes and is applicable equally to organisms which reproduce sexually or asexually.

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A Geneticist on the Taxonomic Method

It seems safe to predict that every reader interested in botany, in the prehistory and history of mankind, in plant geography, or in any related field will thoroughly enjoy Edgar Anderson's fascinating book *Plants, Man and Life* (Boston, Little, Brown and Co., 1952). However, taxonomists of all sorts, be they botanists or zoologists, neontologists or paleontologists, will find additional cause for rejoicing in this book.

For here a great scientist, who considers himself a geneticist (p. 208), sounds in quite unequivocal terms (pp. 207–210, 220) the praises of taxonomy and of the taxonomic method, of the very branch of biology and of the very method which for decades were considered in some quarters matters of the past, especially under the influence of the victorious progress of genetics. According to Anderson, "there is only one branch of biology which is generally equipped to work in such a field [viz., the study of the origin of cultivated plants]. That is taxonomy."

The author then raises the question: "What is the taxonomic method?" Rather than giving a hard and fast definition, he first refers the reader to Marston Bates' book *The Nature of Natural History,* then attempts its definition "by example or by contrasting it with approaches more suitable for other types of problems." By way of a, so to say, negative example, Professor Anderson tells the story of how "one of our very best corn geneticists" failed, owing to lack of personal experience with the taxonomic method, in properly distinguishing two related strains of corn.

The author considers it "difficult to write about the taxonomic method [because] in its broadest aspects it has never been described. Taxonomists are more like artists than like art critics; they practice their trade and don't discuss it." However, "by observing them at work and trying to translate what they were doing to [his] own very different kind of a problem [he] made very much progress."

Taxonomists in general are likely wholeheartedly to agree with two more characterizations of their method given in Anderson's book: The one (p. 210) considers it "one of their simple unwritten axioms . . . that different kinds of things vary in fundamentally different kinds of ways." The other (p. 220) states that "in a taxonomic problem, one has to look here and there for little vestiges of apparent order and work out experimentally from them. . . . He gets on best who has a flexible mind, who does not think in hard and fast terms, who is used to searching through apparently chaotic material for such beginnings of understanding as can be built up in a tentative way." To this we may add: and who does much soul-searching and frequently has recourse to his scientific conscience before reaching a decision on his vexing problems.

OTTO HAAS

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On the Nature of Species in the U.S.S.R.

THEODOSIUS DOBZHANSKY

LYSENKO'S new book * begins with a brief outline of the history of the species concept as developed by Linnaeus, Lamarck, Darwin, and Timiriazev. The two last named authors are mildly reproved for having entertained a theory of "one-sided, flat evolutionism," which assumes that new species arise gradually from old ones, which consorts with the "reactionary pseudo-scientific doctrine of Malthus about intraspecific struggle." This one-sidedness and flatness were done away with by Michurin and by Stalin, who invented "creative Darwinism." The latter "visualizes the development not as a flat evolution, but as a birth in the interior of the old of its opposite new quality, which undergoes a gradual quantitative accumulation of its characteristics, and, in the process of the struggle with the old quality, forms itself into a new fundamentally distinct system of characteristics with its own distinctive law of existence." The clarity of this definition of creative Darwinism is matched by the following definition of species: "A species is a special qualitatively defined status of the living forms of matter. An important characteristic of the species of plants, animals, and microorganisms lies in definite intraspecific relationships among individuals. These intraspecific relationships are qualitatively distinct from the relationships among individuals of distinct species. Hence, the qualitative distinction between the intraspecific and the interspecific relationships is one of the most important criteria for distinguishing between species and varieties." The view that varieties are incipient species is a part of the flat evolutionism. It must be replaced by the view that "species are links in the chain of living nature, or steps of the gradual historical development of the organic world." "The origin and development of new species depends upon such alterations of the metabolism in the process of the development of organisms which involve their species specificity."

If the reader is not profoundly impressed by the above philosophic foundations of "creative Darwinism" he surely can not fail to be so impressed by its experimental verifications. "In 1948 the experiments of V. K. Karapetjan disclosed that some winter sown plants of the hard 28-chromosome wheat *Triticum durum* became rather rapidly, in two-three generations, transformed into a different species, the soft 42-chromosome wheat, *Triticum vulgare*." This splendid success has stimulated even more ambitious undertakings. "In 1949, there was organized a search of seeds of rye in the ears of wheat grown on fields in the foothills of mountains, where the plantings of winter wheat often become contaminated with rye. The source of the contamination of wheat by rye in these localities was not known to science until a few years ago. The investigators V. K. Karapetjan, M. M. Jakubziner, V. N. Gromachevsky, and also several other investigators, agronomists, and students have discovered isolated seeds of rye in the ears of hard as well as of soft

* T. D. Lysenko, *New in the Science of Biological Species* (*Novoe v Nauke o Biologyicheskom Vide*). 30 pp. Selkhozgiz, Moscow, edition of 100,000 copies. Price 30 kopeks. Contains an article on "Species" written for the 2nd Edition of the "Great Soviet Encyclopedia," and a speech on "The Work of the Active Member of the Academy of Medical Sciences, U.S.S.R., O. B. Lepeshinskaia," read at a meeting of the Section of Biological Sciences of the Academy of Sciences of the U.S.S.R. in May of 1950. (1952.)

species of wheat. In 1949 more than 200 such rye seeds were found. These seeds were sown at the Institute of Genetics of the Academy of Sciences of the U.S.S.R., on the experimental field of the V. I. Lenin All-Union Academy of Agriculture Sciences, and at the K. A. Timiriazev Moscow Agricultural Academy. . . . From the rye seeds developed in the ears of hard and of soft wheat there grew, with few exceptions, various but still typical rye plants. Only in a few instances the rye-like seeds gave rise to wheat plants."

The avalanche of discoveries proved hard to stop: "When the branched wheat *Triticum turgidum* was cultivated in the experimental plots of the V. I. Lenin All-Union Academy of Agricultural Sciences, and also in several other places, annually there was observed on these wheat plots contaminations by soft and hard wheats, by oats, by two-rowed and four-rowed barleys, and also by spring rye. All our observations have led us to the conclusion that the source of these contaminants is the branched wheat, *Triticum turgidum*, itself." To be sure, such contaminations were observed in the past, even as far as the first half of the nineteenth century. "But all such discoveries of one plant species in the fields of other species were, as a matter of principle, not considered by scientists as resulting from transformations of one species into another. Always there arose legitimate doubts. The possibility of the contamination being due to the often met with mechanical admixture of seeds could not be excluded. One could not be sure that the seeds sown did not contain some seeds of other species; that seeds of other species were not introduced on the field by water, wind, or by birds; that the contaminant seeds were not conserved for a long time in the soil, etc. . . . To the cases quoted above all the objections just enumerated do not apply. Indeed, scattered rye seeds found in wheat ears which grew for several generations under definite conditions could not be placed in these ears either by birds, or by men, or by any other means. These rye seeds have been produced by wheat plants and have developed in wheat ears."

Further achievements are confidently predicted: "The factual data so far obtained concerning species formation deal with the plant world only. Necessary factual data are still absent about species formation in the animal world. But one may feel certain that the development of the theory of Michurinist biology will in the near future give an opportunity to assemble factual data concerning zoological materials analogous to those concerning botanical ones." To Lysenko, the observations which he reports seem neither startling nor incredible. On the contrary, such things are just what a Michurinist biologist expects. Indeed, "when plants of a given species encounter conditions which are relatively unfavorable for a normal development of their species specificity, there occurs an enforced change, generation in the body of a given species of vestiges of another species, the specific formation of which is more suitable under new conditions of the external environment. The scattered individuals of the new species generated in the interior of the old one are better suited to the new conditions, they multiply rapidly and are capable of displacing the species in the interior of which they were generated." The presence of weeds is thus explained very simply: "Science knew for a long time that many species of weeds exist only in agronomic practice; in free nature these species are not only absent but they are even incapable of existing there. . . . Weed species are generated by some wild species as well as by cultivated species; thus this malignant pest the wild oat [*Avena barbata*] is generated by cultivated oats." "This explains why the wild progenitors of many cultivated plant species have not been found." One wonders at this point whether Lysenko ever heard about the possibility that the environment may, by means of natural selection, induce formation of adaptive genotypes from the genetic elements present in the popula-

tions of the parental species. Or is such an evolutionism too "flat" for him?

He next proceeds to incorporate the wonderful discovery of his fellow Michurinist, O. B. Lepeshinskaia, that cells arise from cell-less materials, into his theory. "Biologists who stand on the Marxian theory of development clearly see the falsity of the postulate that plant and animal cells develop only from cells. . . . If cells arise only from cells, and even from similar cells, then how can an egg cell give rise in the developing organisms to various tissues with most different cells? Moreover, how is the egg cell itself formed? . . . It is absolutely clear to me that no theory of development is possible without acceptance of the view that cells arise from noncellular substances. As stated above, O. B. Lepeshinskaia has demonstrated experimentally that cells not only can arise but regularly do arise in any organism, and especially in the early developmental stages, from matter which has no cellular structure. This postulate and the experimental data obtained by O. B. Lepeshinskaia are basic for understanding many problems of the theory of individual organic development. No less important are the postulate and the experimental data of O. B. Lepeshinskaia for building a true theory of species formation."

"A large body of facts has been accumulated showing that rye may arise from wheat, and that different wheat species may give rise to rye. The same wheat species can generate barley. Rye can also generate wheat. Oats can generate wild oats [*Avena barbata*], etc. All depends upon the environment in which these plants develop. . . . Indeed, it is now completely demonstrated, and anyone interested can easily convince himself, that in the bodies of plant organisms of various species are generated and formed rudiments of bodies of individuals of other species. How does this happen? For example, can one imagine that a cell of the wheat plant becomes transformed into a rye cell? This I can not imagine. This is impossible. We visualize this thing as follows: In the body of a wheat plant, under the influence of proper conditions of life, there are generated granules of a rye body. But this generation does not occur by a transformation of the old into new, in this case, of wheat cells into rye cells, but by way of origination in the inner depths of the body of a given species, from a substance devoid of cellular structure, of granules of the body of another species. To start with, these granules also lack cellular structure, but they give rise later to cells and to rudiments of other species. This is what the works of O. B. Lepeshinskaia contribute toward the theory of species formation. The scientific postulates of O. B. Lepeshinskaia, together with other achievements of science, will form the basis of our developing Michurinian biology."

Lysenko's meteoric career in science has now lasted for almost a quarter of a century. It is most remarkable that during this time neither Lysenko nor any of his followers produced a single new idea, either a right or a wrong one. One might have thought that some original thinking would have occurred almost by accident. Lysenko began by rejection of all the findings of genetics, thus simply falling back to the level of knowledge which obtained in biology toward the close of the last century, which he found conveniently summarized for him in the popular writings of Timiriazev and of other Russian earlier Darwinists. But the grotesque idolatry of Timiriazev and Darwin proved also transient. With the rejection of Darwin's natural selection and of the cell theory, the level of biological knowledge reduces to somewhere back in the first half of the nineteenth century. Lysenko's belief in wheat suddenly generating rye and barley, and vice versa, is harder to date. Evolution through sudden origin of monstrosities was, of course, envisaged by Saint-Hilaire in 1830. But the "granules" which Lysenko imagines to be "generated" in some "depths of the body" sound

(*Concluded on p. 94*)

THIS IS A TRANSLATION of a paper in Russian entitled "Novyie Pogonophora Dalnevostochnykh Morei" which appeared in the Zoologicheskii Zhurnal, Volume 31 (3), pp. 372–391, 1952. No attempt has been made to reword the author's sentences, which abound in colloquial Russian expressions. Only 10 of the author's 27 figures are reproduced here and in these numerals have been substituted for the original Russian characters. The 12 pages of diagnoses of five new species have been omitted partly because our purpose is to acquaint English-speaking zoologists with the general morphology of Pogonophora and the main features of their classification, and partly because all genera with the sole exception of Polybrachia *are monotypic so that identification of genera leads automatically to identification of species. In the case of* Polybrachia *the distinctive characters of the two species are given in connection with the diagnosis of the genus.* A. PETRUNKEVITCH.

New Pogonophora from Far Eastern Seas

A. V. IVANOV

THE Class Pogonophora described by Johansson (1939) is one of the least investigated groups of the Animal Kingdom. Up to the present time we not only do not know the whole plan of structure of these animals, but we cannot even fully visualize their external appearance notwithstanding the fact that almost twenty years have passed already since the discovery of their first representative, *Lamellisabella zachsi* Uschakow. The reason for this is that the Pogonophora live in the ocean at great depths which are difficult of access, or they are barely noticeable and escape observation. Great technical difficulties also attend their study.

Pogonophora—typical denizens of the bottom ooze—lead a sedentary life and secrete around their body a long cylindrical tube which they never leave and which sticks out of the bottom with its open end upwards.

Recent Soviet Oceanographic Expeditions have collected extensive material of Pogonophora whose tubes prove to be extremely numerous in some abyssal localities. Having begun to investigate the new material of Pogonophora which I received from the Institute of Oceanology, Academy of Science, USSR, I was struck by the abundance of new forms in our far eastern seas. Up to recent times only one genus was known—*Lamellisabella,* with two species, *L. zachsi* Uschakow, (1933) and *L. gorbunovi* A. Iwanow,[1] (1949), but I have succeeded in showing (1951) that the long-known *Siboglinum weberi* Caullery (1914) must also be placed here. I now have the opportunity of describing four new genera.

Two circumstances force me to hasten with the publication of the present contribution: first, the great comparative anatomical interest of the Pogonophora, and second, the important position which it seems they must occupy in the characterization of the benthonic groupings of the bathyal and abyssal regions of our seas. I do not propose to give here a complete analysis of the organization of these peculiar animals, but will limit myself provisionally to a description of the external morphology of the new forms.

[1] The author transliterates his name in the German fashion. *A.P.*

For placing this material at my disposal I extend my sincere thanks to L. A. Zenkevitch, J. A. Birstein, and V. L. Vagin.

External Morphology

In view of the fact that up to the present neither description nor figure of the complete animal has ever been given and because all Pogonophora possess identical, very characteristic features, it behooves us first of all to present the fundamental, external morphological peculiarities common to the whole class.

The body of all Pogonophora is distinguished by its unusual length and, in general, cylindrical shape (Fig. 1). It consists of a relatively short anterior section (3) [2] and a very long trunk (13). The former, according to Johansson, is formed by two anterior segments, while the trunk represents the third segment. Correspondingly there are three pairs of coelomic sacs; the small anterior pair (Fig. 7:38) contains nephridia, the second is connected with the coelomic cavities of the tentacles, the third contains the gonads.

Characteristic is the well-developed apparatus of the tentacles or hands (1) attached to the anterior end of the body. The tentacles bear rows of very small pinnules and undoubtedly perform a respiratory function because they are supplied with blood vessels. Perhaps they serve also as an apparatus for passive collection of food (nannoplankton and detritus).

The anterior section of the body is separated from the trunk by an external ring-shaped constriction (5) and by an internal muscular diaphragm. Dorsal to the base of the tentacles, the anterior section is drawn out into a medial lobe which contains the brain and which I shall call provisionally the cephalic lobe (Fig. 2:19). On the ventral surface of the anterior section there is always present a pair of oblique, medially converging, cuticular ribs or combs which I shall call the bridle (frenulum, 4) and which probably serves as a support on the edge of the tube when the animal protrudes the anterior end of its body. The combs attenuate gradually as they pass forward toward the lateral surfaces of the body and then onto its dorsal surface.

The trunk, which is here fully described for the first time, changes considerably from the anterior to the posterior end. Two main sections can be clearly recognized in it. The anterior one, which I shall call the preannular section (11), extends as far as the special belts (annuli, 14), while the posterior or postannular section (16) lies behind them.

The preannular section bears, anteriorly, a fairly wide ventral groove (6) which gradually becomes obliterated toward the posterior end. The groove is bordered on its sides by small folds which bear rows of adhesive papillae (10) on which small, rounded or pear-shaped elevations are situated, little cushions supplied with tiny chitinized platelets (9). The platelets are wanting only in *Siboglinum.* The animal probably clings by means of these small cushions with platelets to the inner surface of the tube when moving in its cavity.

Anteriorly the disposition of the organs of attachment is characterized by fairly regular metamerism which can only be regarded as secondary. However, the further back, the more the metamerism becomes disturbed until the adhesive papillae become scattered irregularly, although limited as before to the ventral surface. The greater portion of the preannular region is characterized by just such an irregular distribution of adhesive organs. Thus in the preannular region we can distinguish a short metameric portion (7) and a very long non-metameric one (12).

In addition, the integument of the preannular region of the trunk is characterized by a broad, dorsal, ciliated band (Fig. 4*B*:28), which begins immediately behind the muscular diaphragm and usually extends to the end of the metameric region. Apparently it is a sense organ (perhaps a chemoreceptor), judging by its connection with the dorsal nerve trunk.

Two belts (14) of chitinous platelets are

[2] Numbers in parentheses refer to those on figures. *A.P.*

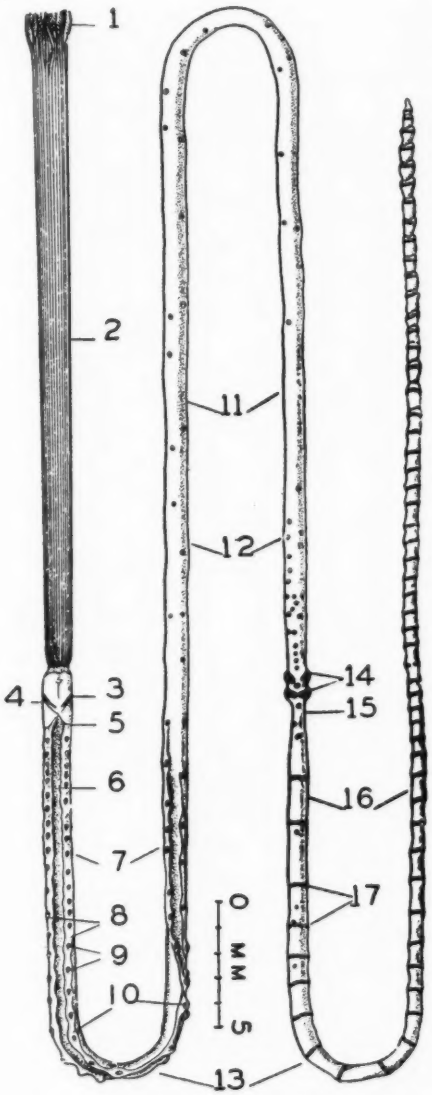

FIG. 1. *Lamellisabella zachsi* Uschakow. Ventral view of female, combined from several specimens.

KEY TO NUMERICAL SYMBOLS OF FIGS. 1–8

1. Pinnules
2. Tentacles
3. Anterior section of body
4. Bridle (frenulum)
5. Ring-shaped constriction between anterior section of body and trunk
6. Ventral groove of metameric region
7. Metameric region of preannular section of trunk
8. Ventral folds of metameric region
9. Adhesive platelets
10. Adhesive papillae
11. Preannular section of trunk
12. Non-metameric region of preannular section of body
13. Trunk
14. Belts
15. Constriction of trunk behind belts
16. Postannular section of trunk
17. Transverse row of adhesive papillae
18. Transverse grooves of anterior section of body
19. Cephalic lobe
20. Anterior part of anterior section of body
21. Posterior part of anterior section of body
22. Genital papilla of male
23. Medial pit
24. Rings of anterior section of body
25. Medial groove
26. Medial fold of anterior section of body
27. Papilla (one of pair limiting ventral emargination of ring-shaped groove)
28. Dorsal ciliated organ
29. Brachiophore
30. Outer edge of tentacular plate
31. Tube
32. Optical section of turns of spiral of tentacular plate
33. Lophophore
34. Row of tentacles
35. Base of lophophore
36. Base of tentacles
37. Longitudinal musculature
38. Anterior pair of coelomic sacs
39. Body wall
40. Tubiparous glands
41. Filament
42. Prolongation of spermatophore
43. Thickened portion of filament of spermatophore

situated behind the middle of the trunk section of the body. They girdle the trunk in a more or less oblique direction, usually parallel to each other and interrupted on the ventral surface. Their ventral ends are directed obliquely backward. Each belt (annulus) consists of rows of very small, oval, chitinoid, annular platelets

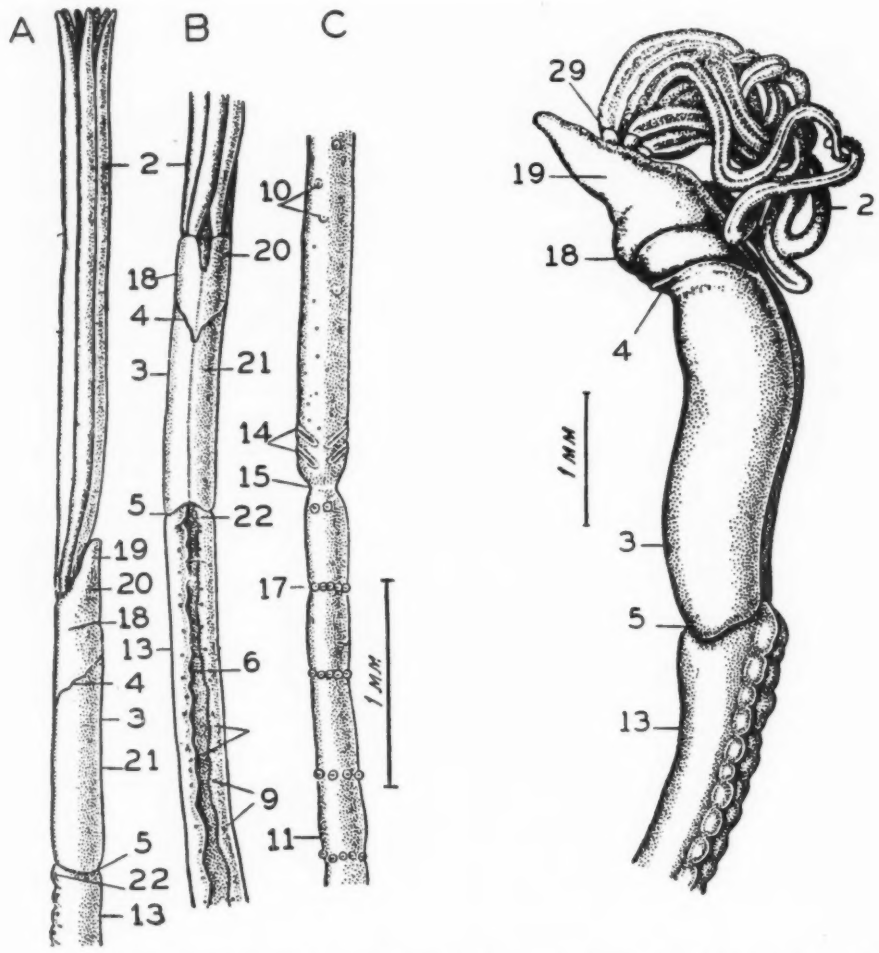

FIG. 2. *Heptabrachia abyssicola*, gen.n., sp.n.* Male. *A*, anterior end viewed from left side; *B*, ventral view of anterior end; *C*, Region of belts with adjacent portions of preannular and postannular sections of trunk viewed from ventral side.

FIG. 3. *Birsteinia vitjasi*, gen.n., sp.n. Male. Anterior end of body viewed from right side.

*All names of species, genera, and families thus indicated as new were, of course, proposed in the original (Ivanov, 1952), *Ed. note.*

the surface of which is covered with microscopic denticles. The belts are on skin folds or elevations and serve for firm fixation of the median portion of the body inside the tube when, as one may imagine, the disturbed animal withdraws the anterior end of its body with the tentacles into the tube by a sudden contraction of the longitudinal musculature.

Behind the belts there is usually a considerable constriction (15), posterior to which the postannular region begins. The latter has a more or less cylindrical shape and also bears small, adhesive papillae with chitinoid platelets. But here these organs are again arranged metamerically (16), forming transverse rows on the ventral surface of the body (17). Because of

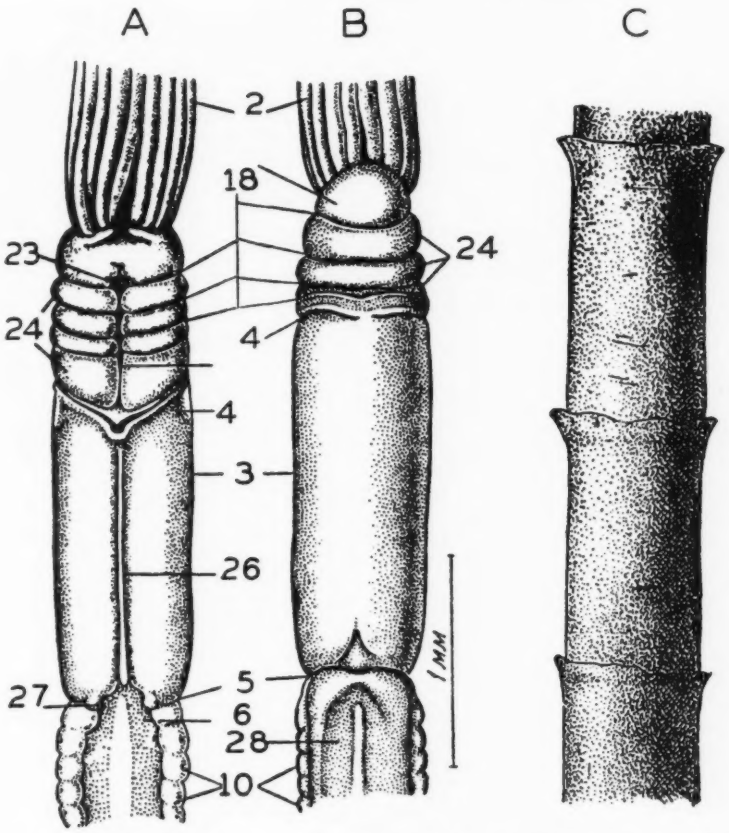

FIG. 4. *Polybrachia annulata*, gen.n., sp.n. *A*, ventral view of anterior end of female; *B*, dorsal view of anterior end of female; *C*, anterior end of tube.

this the entire postannular region of the body gives a false impression of segmentation.

Thus, the anterior portion of the preannular region as well as the entire postannular region exhibits a clearly expressed, secondary, external metamerism. But it has a different character at its anterior end from that at its posterior.

As yet I have been unable to find either the oral or the anal opening in any representative of Pogonophora.

Investigation showed that all Pogonophora have separate sexes. Externally the males do not differ from the females in any substantial way. The only external difference consists in the presence of a pair of genital papillae in males. These are situated on the border between the anterior section of the body and the trunk (Fig. 2:22), and bear the external openings of the sperm ducts. The latter are a pair of long canals which occupy a considerable portion of the preannular region and are usually filled with characteristic spermatophores. The structure and shape of the spermatophores vary greatly in different genera.

The characters of greatest taxonomic importance are the tentacles, the form and dimensions of the adhesive platelets and of the bridle, as well as the shape of

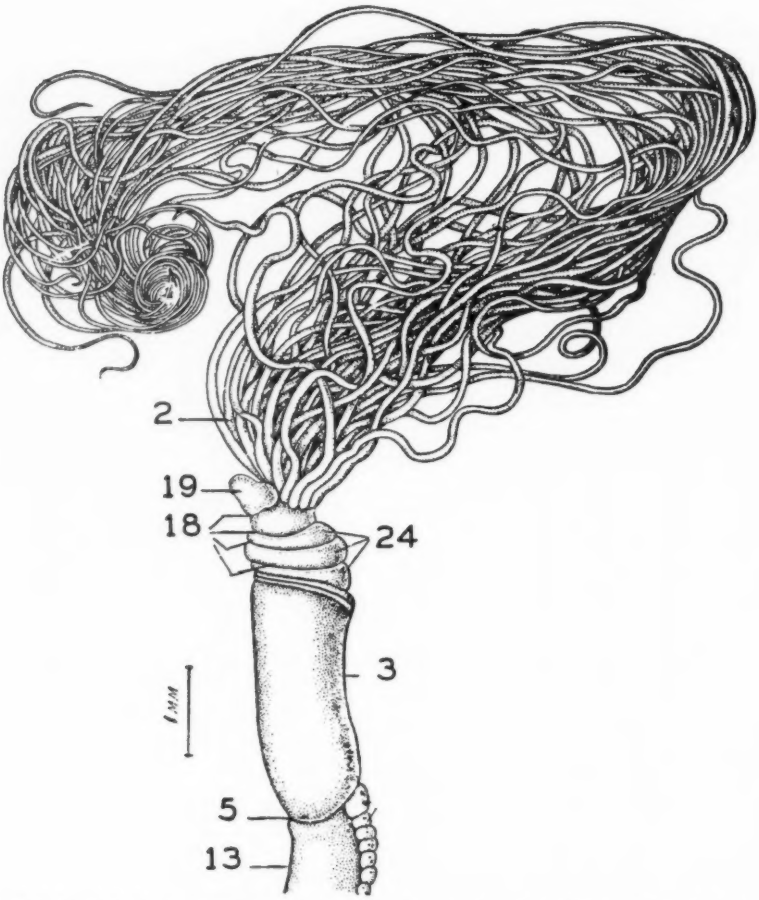

FIG. 5. *Polybrachia barbata*, gen.n., sp.n. Anterior end of male viewed from right side.

the various portions of the body. Especial importance attaches to the tentacular apparatus.

Possessing a powerful longitudinal musculature (Fig. 7:37), the animals strongly contract on fixation. For this reason individuals fixed in the tube usually have a different appearance and different body proportions from specimens removed from their tubes before fixation.

The tubes of the Pogonophora (Fig. 4*C*) never branch, consist of a chitin-like organic substance, and have a lamellated structure, wherein they differ sharply from the thecae of graptolites and pterobranchs, which according to Kozlowski (1947), are composed of characteristic half rings. In general the tubes are similar in all Pogonophora, but the details of their structure may be used for the characterization of different forms.

The Class Pogonophora undoubtedly belongs to the Deuterostomia and most likely represents a separate type with the Enteropneusta and Pterobranchia.[3]

[3] A similar opinion was recently expressed by Beklemishev (1951). I postpone a more definite judgment on this subject until the completion of investigations dealing with the internal structure of these animals.

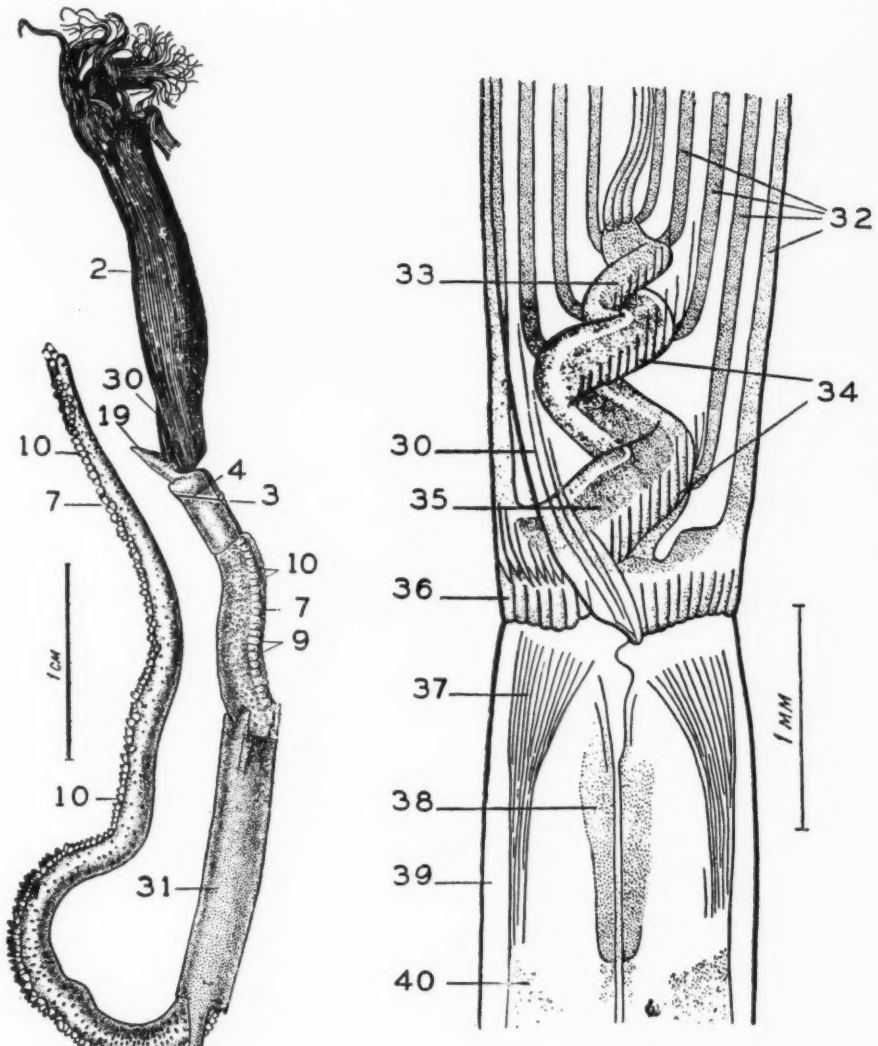

FIG. 6. *Spirobrachia grandis*, gen.n., sp.n. Anterior portion of female viewed from right side.
FIG. 7. *Spirobrachia grandis*, gen.n., sp.n. Anterior end of male viewed from ventral side.

[The following twelve pages of the Russian text contain detailed descriptions of five species and are omitted here. The species are: *Heptabrachia abyssicola, Birsteinia vitjasi, Polybrachia annulata, Polybrachia barbata,* and *Spirobrachia grandis.*]

Diagnoses of Genera

1. *Heptabrachia* A. Iwanow, gen.n. Pogonophora with seven free tentacles the bases of which are arranged in a closed circle. Anterior portion of body in front of the bridle with a transverse groove.

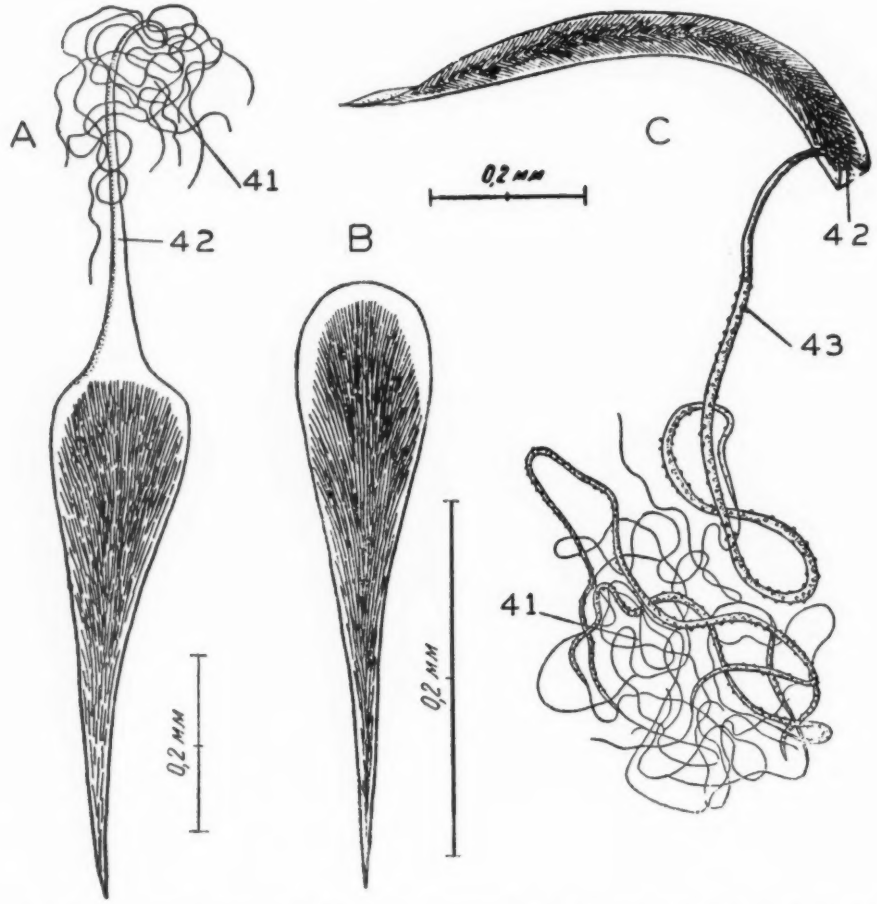

FIG. 8. Spermatophores: *A, Polybrachia annulata; B, Heptabrachia abyssicola; C, Birsteinia vitjasi.*

Combs of bridle merge medioventrally. Adhesive platelets of preannular region round, with a sickle-shaped thickening of their anterior edge; in postannular region, rod-shaped. Spermatophores small, leaf-like, drawn out at one end to a point, without a filament. (Fig. 8*B*).

A single species, *H. abyssicola* A. Iwanow, with the characters of the genus. A single specimen. Northwestern region of Pacific Ocean. Depth 8100 meters. (Fig. 2.)

2. *Birsteinia* A. Iwanow, gen.n. Thirteen, free tentacles with brachiophores, attached to the body in a circle. Anterior section of body (Fig. 3) in front of the bridle with a sharp annular groove. Combs of bridle fused medioventrally. Adhesive platelets small, oval. Spermatophore (Fig. 8*C*) elongated, not flattened, with a long filament partly covered by granules of secretion.

A single species, *B. vitjasi* A. Iwanow, with the characters of the genus. Four males. Behring Sea. Depth 3820–3830 meters.

3. *Polybrachia* A. Iwanow, gen.n. Numerous, long, free tentacles attached to a

horseshoe-shaped base, the ends of which are directed toward ventral surface. Anterior section of body in front of the bridle divided into several rings (Fig. 4, *A, B*). Combs of bridle do not merge medioventrally. Adhesive platelets on anterior portion of trunk small, oval. Spermatophores (Fig. 8*A*) leaf-shaped with a ribbon-like prolongation which continues as a very thin filament.

Two species. (1) *P. annulata* A. Iwanow. With 39 tentacles. Anterior section of body with four rings. Ten specimens. Behring Sea. Depth 3330 meters. (2) *P. barbata* A. Iwanow (Fig. 5). With 71 tentacles. Anterior section of body with two rings. A single specimen. Behring Sea. Depth 3820–3830 meters.

4. *Spirobrachia* A. Iwanow, gen.n. More than 200 very long tentacles united into a plate which is spirally wound as a roll of paper (Figs. 6, 7). Bases of tentacles arranged in a screw-spiral attached to a lophophore (33). Anterior section of body not divided. Combs of bridle not fused on ventral surface, but united on back. Adhesive platelets large, with an arc-shaped thickening. Spermatophores very large, leaf-like, with a pointed end and a thick filament.

A single species, *S. grandis* A. Iwanow, with the characters of the genus. Two specimens, male and female. Behring Sea. Depth 3330 meters.

General Considerations

The data concerning the external morphology of Pogonophora which have been presented above permit one to draw certain conclusions, although, naturally, wide comparative anatomical conclusions will be possible only after a study of their internal organization.

One of the basic problems is the segmental composition of the body. A study of sections through the trunk confirms Johansson's opinion concerning the presence of three segments in the body of Pogonophora. The two anterior segments —the first and the second—form by fusion the anterior section of the body and are correspondingly homologous with the proboscis (cephalic disc) and the collar of the Enteropneusta and Pterobranchia. The trunk of the Pogonophora is represented by the third segment and corresponds to the trunk of the Enteropneusta and Pterobranchia. The sharply defined annular groove which in some forms (*Birsteinia, Heptabrachia,* and *Polybrachia*) lies in front of the bridle is probably an external sign of the primary segmentation of the anterior section of the body.

The secondary metamerism of the external organs was developed independently of the primary segmentation. It involved the organs of adhesion on the anterior portion of the preannular region and on the entire postannular region. A similar, purely external, secondary character is presented by the annulation of the anterior region in *Polybrachia.* Further back the metamerism of the adhesive papillae becomes unstable. Even where it is manifested at its best, it is frequently incomplete and subject to disarrangement and to individual variation. Such instability is correlated with a gradual transition within the limits of the preannular section from a metameric arrangement to a disorderly one. All this indicates that we have before us a typical example of an as yet incomplete orderly arrangement of numerous organs which originally were scattered in disorder, i.e. one of the usual ways in which metamerism in animals has had its origin (Beklemishev, 1944).

The secondary metamerism of the trunk-segment is known to be characteristic also of Enteropneusta (gill slits, hepatic diverticles of the gut, gonads). Evidently the tendency for its formation is generally characteristic of the lower Deuterostomia which have retained in their adult state the trisegmental composition of the body and which have a very elongated third segment. In the opinion of many authors the maximal development of this peculiarity in the Chordates led to a splitting up of the third segment (the trunk) into a series of secondary segments. Thus the metameric disposition of the organs of adhesion in Pogonophora,

along with other traits of their organization, point to their belonging to the Deuterostomia.

A comparison of the tentacular apparatus in different genera is of considerable interest. The number of tentacles varies within wide limits: *Siboglinum* has a single tentacle; *Heptabrachia,* 7; *Birsteinia,* 13; *Lamellisabella,* 29; *Polybrachia annulata,* 39; *Polybrachia barbata,* 71; and finally *Spirobrachia,* 223. At present it is difficult to decide whether the presence of a single tentacle in *Siboglinum* represents the most primitive state, or is a manifestation of secondary oligomerization. All the other genera form an orderly series according to the number of their tentacles. It is true that in forms with numerous tentacles (*Polybrachia* and *Spirobrachia*) their number may possibly be subject to individual variations, but not to such an extent as to change the general picture of a consecutive increase in number of these organs, parallel with an increase in complexity of their organization. Evidently we have before us a typical case of polymerization of organs (Dogiel, 1947).

In forms with a small or intermediate number of tentacles, namely in *Heptabrachia, Birsteinia,* and *Lamellisabella,* these organs are attached to the body in a circle. Evidently such a circular arrangement is the primitive one, if one leaves out of consideration *Siboglinum* with its single tentacle. Subsequently, with an increase in the number of tentacles, there takes place a change in the base of the crown. The circular line of attachment of the tentacles becomes horseshoe-shaped and, because of this, bilaterally symmetrical. With this arrangement the number of tentacles can be increased in the limited area of the anterior end. However, in *Polybrachia annulata* this method of increase in number is correlated with another, namely that the tentacles, instead of being arranged in a single row, have by alternating with one another become arranged in two or even in three rows. This peculiarity is still more strongly manifested in *P. barbata* in which the tentacles occupy the entire surface of the horseshoe-shaped base of the crown.

We find a quite different solution of this problem in *Spirobrachia.* Here a break in the primary circle of the tentacular bases apparently has taken place on the ventral surface of the body. This made a considerable increase in the number of tentacles possible by way of a spiral arrangement, the elongation of the spiral having probably taken a centripetal direction. It seems that in *Spirobrachia,* even this method of development proved to be insufficient and the requirement for a still greater number of tentacles was met by their arrangement in a screw (Fig. 7). In connection with this a new structure appeared—a screw-shaped outgrowth of the body—the lophophore (33) situated inside the base of the crown.

Thus all Pogonophora with the exception of *Siboglinum* fall into groups with the base of their tentacular crown either circular, horseshoe-shaped, or spiral.

Two genera, *Lamellisabella* and *Spirobrachia,* are distinguished by a fusion of the tentacles so that only the distal ends of the latter remain free. In *Lamellisabella,* which has a circular disposition of the tentacles, there is thus produced a long, hollow tentacular cylinder, while in *Spirobrachia* a spiral tentacular plate is formed. Finally *Birsteinia* is characterized by a differentiation of the tentacular bases in the shape of small brachiophores. In this way the tentacular apparatus varies greatly in different genera, while the other peculiarities of their organization, not to mention the general plan of structure, are very uniform, bespeaking a great homogeneity [4] of the entire group.

Many traits of the external morphology of Pogonophora point to strong specialization induced by a sessile mode of life. Such are the tentacles at the anterior end of the body, and the ability to secrete a tube (with the presence of which the extraordinary elongation of the body is cor-

[4] Ivanov uses the expression "monolithic state." *A.P.*

related), as well as all kinds of adaptations which facilitate movement within the tube (the bridle, adhesive papillae, belts with their toothed platelets). It is probable that the adhesive papillae were originally scattered irregularly over the entire trunk. Later, in connection with the character of their function, there took place a metameric readjustment of their disposition, which appeared also as an adaptation to life in a tube. As a result of the sedentary mode of life the Pogonophora acquired the appearance characteristic of a series of sedentary animals inhabiting tubes (Phoronida, sedentary Polychaeta, Pterobranchia).

On the basis of everything presented here I consider it possible to distinguish the following four families:

1. Siboglinidae Caullery, 1914. Pogonophora with a single tentacle. Adhesive papillae without platelets. Genus *Siboglinum* Caullery, 1914.[5]

2. Polybrachiidae A. Iwanow, fam.n. Pogonophora with numerous free tentacles arranged in a circle or on a horseshoe-shaped base. Genera: *Heptabrachia, Birsteinia, Polybrachia.*

3. Lamellisabellidae A. Iwanow, 1951. Pogonophora with fused tentacles forming a hollow cylinder. Genus *Lamellisabella* Uschakow.[6]

4. Spirobrachiidae A. Iwanow, fam.n. Pogonophora with fused tentacles forming a tentacular plate rolled up spirally. A lophophore wound in the form of a screw is present. Genus *Spirobrachia.*

[5] For description and figures of the single species, *S. weberi,* see Caullery (1914 and 1948). *A.P.*

[6] Translator's note: According to Ivanov (1949), *Lamellisabella gorbunovi* Iwanow differs from *L. zachsi* Uschakow (Fig. 1) by the following characters. (1) Poor development of oblique, chitinized platelets of anterior section of body and their position in anterior half. (2) Oval or rounded shape of papillae of adhesive organs of posterior section. (3) Elongate, rod-shaped, chitinous platelets of adhesive organs. (4) Simple, circular groove between anterior and posterior sections of body. (5) Peculiar structure of tube, having the appearance of stacked funnels. Polar Sea. Depth 3700 meters. *A.P.*

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ARIZONA
DISTRIBUTION
MAP
U T A H
N E V A D A
C A L I F O R N I A
N E W M E X I C O
LEGEND
SPRING
WELL
LAKE
PLAYA
DAM
SPECIMENS EXAMINED
LITERATURE RECORD
RESERVOIR
INTERMITTENT
Spring, 1950
0 10 20 30 40 50
SCALE IN MILES

A Drainage Map of Arizona

ROBERT RUSH MILLER

BIOLOGISTS concerned with illustrating the distribution of aquatic or semi-aquatic organisms or of life associated with streams often find it difficult or impossible to obtain accurate drainage maps of the area of their interests. This has proved to be a particular problem for students of fish distribution and has made necessary the special drafting of such maps. The accompanying drainage map of Arizona is presented here with the belief that others may find it useful in their studies.

The base used for the map is the *Topographic Map of the State of Arizona,* prepared by N. H. Darton and published by the Arizona Bureau of Mines (University of Arizona) in cooperation with the U. S. Geological Survey (printed 1923, revised 1933). Field observations made during the summers of 1938 and 1939 and from March 21 to June 16, 1950, over most of the state, provided the basis for determining changes that have taken place in water conditions. Except for the northeastern region, where reliance was placed largely on Gregory (1916, *The Navajo Country,* U. S. Geol. Surv., Water-Supply Paper 380), surface waters shown are believed to represent a reasonably accurate picture of conditions in the spring of 1950. Much local testimony also contributed to the hydrographic picture. In particular I am grateful for information from Harold S. Colton (Director, Museum of Northern Arizona), Harold C. Bryant (Director, Grand Canyon National Park), and R. D. Holtz (Superintendent, Fort Apache Indian Reservation). The topographic quadrangles of the U. S. Geological Survey, the National Forest maps of the U. S. Forest Service, and the map of the Fort Apache Indian Reservation (U. S. Office of Indian Affairs, 1938) also were consulted. The outlines of recent reservoirs (constructed subsequent to Darton's map) were taken in large part from *The Colorado River* (U. S. Bureau of Reclamation, March 1946).

The necessary field work and the drafting of the map were supported by a research grant from the Horace H. Rackham School of Graduate Studies of the University of Michigan. The map was drafted by William L. Cristanelli, to whom much credit is due. My wife, Frances H. Miller, assisted me in the painstaking checking of the several drafts.

More than one-half of Arizona now lacks permanent surface waters and is classed as desert, with an average annual rainfall of less than 10 inches. It was not always so dry, however, and the Gila River once was a perennial stream from east to west across the state. Over most of its length it is now reduced to a sandy wash that comes to life only in exceptionally wet years. The reduced flow of Arizona's surface waters is due, in large measure, directly or indirectly to man's activities. Aside from the Colorado River, the major area of permanent water is concentrated in the high mountains (up to 11,600 feet) of the east-central part of the state.

Some of the smaller stretches of permanent streams, lakes, and reservoirs have been represented as lengthened or enlarged beyond their actual size, in order that they may be visible on the map. It was not feasible to show the complicated pattern of irrigation canals of the Salt River Project in the Phoenix area or of those around Yuma.

Copies of the map (12¼″ x 15¼″) may be purchased by writing to the Secretary, Museum of Zoology, University of Michigan, Ann Arbor, Michigan. The cost is 50 cents for one copy and 15 cents for each additional copy up to a dozen copies. Special rates are available for requests of 12 to 100 copies. One hundred may be purchased for $5.00. Make checks payable to: Museum of Zoology, University of Michigan.

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Distribution Patterns and Phylogeny of Some Western Ground Squirrels

STEPHEN D. DURRANT and RICHARD M. HANSEN

IT IS well known that many kinds of mammals attain their distributional limits in the intermontane West. In Utah in particular many species reach their limits, and along the margins of the ranges, many small populations have developed under semi-isolation into recognizable subspecies in relatively short periods of time. We have been making a detailed study of ground squirrels of the subgenus *Citellus* (Oken) for the past several years. The study of taxonomy and speciation has to date been largely restricted to data concerning the morphological features of the animals. While plotting the ranges of these species, and studying competition between different species at the interphases of their ranges, we have made many observations which lead us to believe that a significant supplement to the morphological data may be obtained by field studies of the distribution and ecology of related species under intense competition. Within the given genus, what are the relationships as indicated between degrees of allopatry and sympatry? What does competition indicate about the rate of differentiation and selection?

The ground squirrels of North America belong to the genus *Citellus* and are divided into eight subgenera. The group here reported upon is that of the shorttailed ground squirrels of the subgenus *Citellus* (Oken). We are not concerned at present with all the species of this subgenus, but only with the following: *C. armatus, C. beldingi, C. richardsoni, C. columbianus,* and *C. townsendii* and its allies. Generally speaking *C. armatus* is a northern species that attains its southern limits in Utah; *C. beldingi* is a northwestern species that attains its southeastern limits in Utah, in the extreme northwestern part of the state; *C. richardsoni* is a northern and eastern species that has its southern limits in Colorado and Utah and its western limits in Nevada; *C. columbianus* is also a northern species that extends as far south as southcentral Idaho; and *C. townsendii* and its allies are western and northern animals that extend as far east as central Utah (Fig. 1).

Students of these shorttailed ground squirrels are familiar with the fact that within their ranges they occupy several types of habitats ranging from dry hillsides to lush, moist meadows. Members of all of the aforementioned species apparently prefer moist, lush meadows when they are available. Within the ranges of the several species of this subgenus, members of each species always occupy a wider variety of habitats if that species is the only representative of the subgenus present.

Intraspecific competition appears to be of lesser degree than does interspecific competition. We have noted that where the ranges of *C. richardsoni* and *C. armatus* come into contact in Rich and Daggett counties, Utah, each species occupies a narrower variety of habitats than it would if it occurred there alone. At these localities, where the ranges of the two come into contact, colonies of *C. richardsoni* occupy the dry, open areas between stands of sagebrush and greasewood, while those of *C. armatus* occupy the grassy meadows. It is noteworthy that at this zone of contact between the ranges of these two species, the competition is extreme; the burrows and feeding areas of the animals of one species being in some instances but a

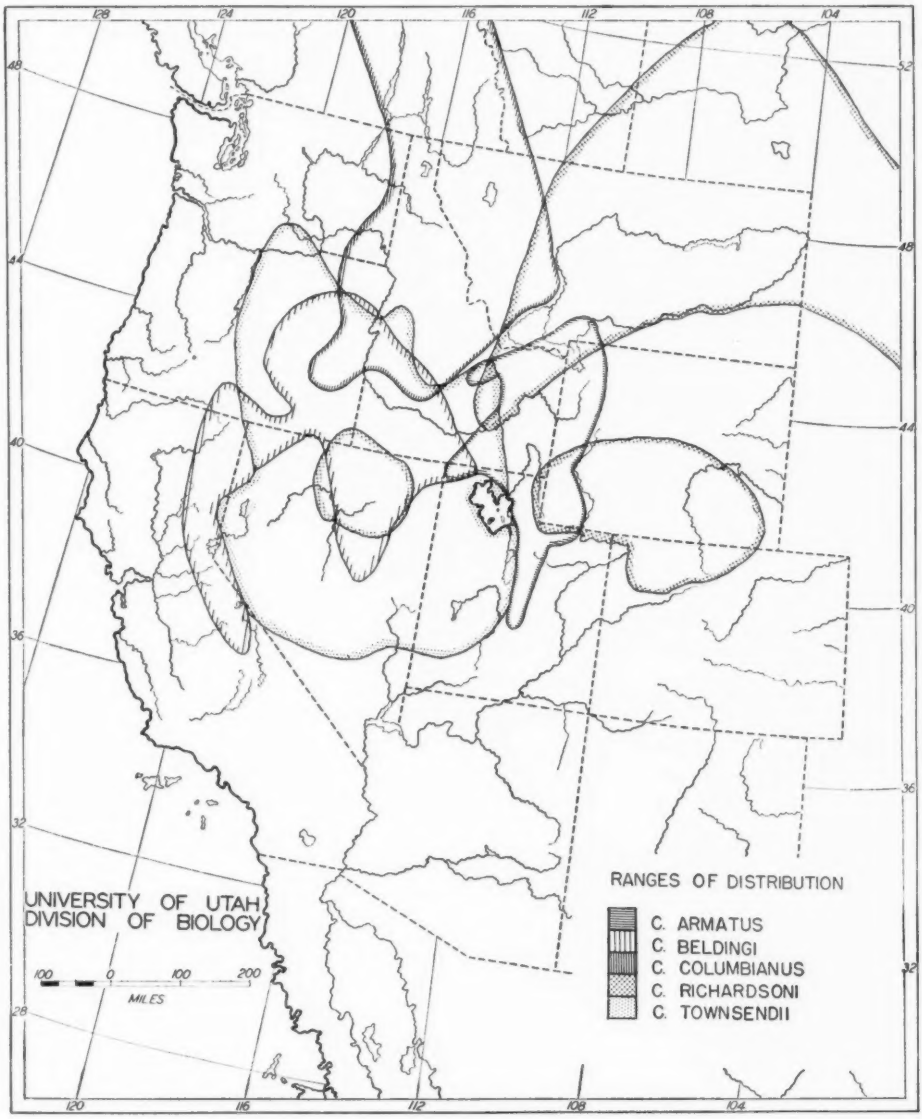

FIG. 1. Distribution of the species of the subgenus *Citellus* (Oken) in the intermontane region of western U. S.

few feet from those of the other. Back from the zone of contact between the ranges of these two species, we noted that where animals of only one of the two species occurred, they lived in both the wet and dry situations, indicating that they could live successfully in either wet meadows or dry, barren ground as long as members of the competing species were not present.

In Colorado, Warren (1942, p. 124) reported colonies of *C. richardsoni* as occurring in high mountains, and that in some instances they had crossed over passes at 11,000 feet to become established in the heads of drainages on the other side of the mountains. Since members of a competitive species do not occur in these mountains in Colorado, colonies of *C. richardsoni* were able to establish themselves there. In the western part of the Bridger Basin the ranges of *C. armatus* and *C. richardsoni* overlap. Where both are found together here, they are ecologically displaced as previously noted. Each lives, however, in wet, moist areas and also in dry, semiarid areas in the Bridger Basin, except where colonies of the two co-exist. In Idaho, Davis (1939, pp. 171–180) reported the same relative ecological distribution for colonies of *C. armatus* and *C. richardsoni* as we have noted, and commented that they both occupy the same types of habitats; but he did not indicate whether or not the animals of the two species are ecologically displaced when they occur together. We suspect that they are. Apparently ground squirrels belonging to *C. richardsoni* are better adapted to dry soils than are those of *C. armatus*, but since both are known to survive in the same range of ecological habitats, it is competition that limits their ranges where they meet. In the Grouse Creek area of northwestern Utah, where colonies of *C. armatus* and *C. beldingi* come into contact with each other, we noted that the animals of *C. armatus* occupied the dry localities, while those belonging to *C. beldingi* occupied the wet meadows. In Idaho, Davis (1939, pp. 169–172) reported that animals of these two species occupy the same habitats, and that the ranges of the two species overlapped there, but he did not note whether or not they were ecologically displaced, although he found them in separate colonies in the same field. He did state that animals of both species prefer moist meadows, although both will live in dry areas, and this is in agreement with our findings in Utah. Apparently animals of *C. armatus* are better adapted to dry situations than are those of *C. beldingi.*

In Utah, we have not found colonies of *C. townsendi* in close proximity to those of *C. armatus* and *C. beldingi,* but we have found them about a mile apart. Our observations indicate that in these localities, ground squirrels of the species *C. townsendii* lived in extremely dry habitats, drier than any found for the other two aforementioned species. In Idaho, however, north of the Snake River in Jerome County, we did find animals of *C. townsendii* living on the dry soils while the adjacent meadow was occupied by animals of *C. beldingi.* We noted animals of *C. beldingi* also on dry soils, but only in the absence of *C. townsendii.* It is evident that animals belonging to the species *C. townsendii* are remarkably well adapted to life in extremely dry areas.

Hall (1946, p. 290) reported that wherever *C. beldingi* and *C. townsendii* were found together in Nevada, the Belding ground squirrel occupied the meadowland, and colonies of *C. townsendii* lived on the sagebrush-covered benches. He further commented on the fact that both of these kinds of ground squirrels prefer moist situations, but he did not comment on what happens where the ranges of *C. richardsoni* and *C. townsendii* overlap.

To date, the Belding ground squirrel has not been taken north of the Snake River in Idaho. We found both the Columbian and Belding ground squirrels north of the river. In this region, they both occurred in the moist meadows. We

did not have an opportunity to observe them in the same locality, but we are of the opinion that where their ranges overlap, the Belding ground squirrel will be found to occupy the moist habitats, while the Columbian will be found in the drier situations.

Phylogenetic Interpretation

Since all members of this subgenus are of generally northern occurrence, attaining their southern limits in the western states, and since all prefer moist habitats where available, it would seem that the adaptational feature essential to increasing the range to the southward would be the ability to take over more xerophytic situations. From our observations on competition between the several species, we align them with reference to this adaptation in the following order: first, *C. townsendii* is able to outcompete any other for arid places; next is *C. richardsoni,* followed by *C. armatus,* then *C. columbianus,* and finally by *C. beldingi* which is the least adapted to dry conditions. These observations are somewhat borne out by studies on the areas of occurrence. It is axiomatic in the study of mammals that the subspecies of a species are all allopatric. Therefore, within limits, it would appear within a genus or subgenus, that the greater the amount of allopatry between the full species the younger the genus. Moreover, the greater the amount of sympatry between species of the genus, the greater the divergence between the species, hence the older the genus. The subgenus in question has some sympatry, but in general is markedly polymorphic and allopatric. Some species are totally allopatric with reference to other species; some have only a minor degree of overlap of ranges and in only one case are the ranges markedly sympatric. The ranges of *C. townsendii* and *C. beldingi* are sympatric to a large extent, and the animals are markedly distinct in both morphological and ecological characteristics. The ranges of *C. beldingi* and *C. armatus* are practically allopatric and the animals are quite similar in both morphology and ecological tolerances. With the exception of the subspecies *C. r. nevadensis,* the ranges of the species *C. beldingi* and *C. richardsoni* are totally allopatric. The subspecies *C. r. nevadensis* is a relict and is on the way out. Its range is sympatric with both *C. beldingi* and *C. townsendii.* The former outcompetes it for the wet situations while the latter does the same with reference to the dry ecological situations. In comparing the ranges of each species with all others, it is apparent that there is a correlation between the degree of overlap of the ranges, the morphological relationships and the ecological tolerances of the animals of the species in question.

From the above data on interspecific competition, and from our study of the degree of sympatry and allopatry of the ranges of these species, we would formulate a phylogeny of the members reported upon in this subgenus in the following manner: *C. townsendii* is the most divergent, next *C. richardsoni,* then *C. armatus,* with *C. columbianus* and *C. beldingi* being more conservative and closer to the ancestral type. Furthermore, these conclusions are in keeping with the known history of animals of this region with reference to the happenings of Pleistocene and post-Pleistocene time.

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Points of View

Notes on Nomenclature and Classification

Athough nomenclature and classification are two separate subjects, they interact with each other in many ways. It is nomenclature in particular which is often affected by changes in taxonomic thinking and procedure, such as the introduction of the polytypic species or that of the type method. At the Fourteenth International Congress of Zoology at Copenhagen in August 1953 a sincere effort was made to eliminate so far as possible previously existing conflicts between the two fields. Nevertheless many issues are left which require further clarification. The object of the present note is to introduce three subjects which may benefit from further discussion. It is my impression that our thinking on these topics has not yet reached complete clarity.

(1) *Stability and the binomen.* Many of the new provisions in the rules of zoological nomenclature that were adopted at Copenhagen have the avowed purpose of insuring greater stability of nomenclature. This is welcomed by all zoologists, but it raises the question of the ultimate limits of stability. It appears from statements in the recent literature that some taxonomists do not realize that the fact of binominal nomenclature itself sets definite limits to the degree of stability that can be achieved. The stability of specific names and that of generic names can be regulated by rules of nomenclature. The stability of the combination of both, namely, that of the binomen, depends on the stability of zoological classification. Stability of the binomen, then, depends on the finality of zoological classification on the generic level.

It is often forgotten that the scientific name of a species, by consisting of two parts, serves two functions. Binominal nomenclature was introduced by Linnaeus in order to permit both of these functions. The objective of the specific component is that of recognition. It is for this reason that the specific name must be unique and that it should be of the greatest possible stability in time and universality in space. One specific name should refer to only one species and this species should be known at all times under only one name. Many of the rules of zoological nomenclature have as their principal object the achievement of as close an approach to the stated ideal as is possible.

The function of the generic component of the binomen, however, is very different. A "generic" name—in taxonomy as in daily life—classifies. The object of the generic name, then, is to label groups of species believed to be "related." Taxonomic arrangements thus are the result of judgements which in turn are based on the available evidence. The delimitation of genera, thus, is a zoological task, the stability of which is evidently limited. Every addition to our zoological knowledge may result in a revision of classification and a consequent alteration of the binomen.

In ornithology we are at the present time in the awkward and unpleasant situation of having to give up many well-known binomens. The reason for this is that between the years 1830 and 1860 there was a rage of generic splitting (largely for quite irrelevant philosophical reasons) leading to the prevalence of monotypic or nearly monotypic genera in certain families. Recent revisers have pointed out the zoological invalidity of many of these so-called genera and have taken the logical step of eliminating those that have no scientific foundation. It seems to me

that the protests that have been lodged against such actions are based on a misunderstanding of the above-discussed difference in the function of the two components of the scientific name. It is now generally admitted that stability is one of the chief objects, if not the principal one, of zoological nomenclature. However, I cannot see how such stability can be extended to a binominal combination if this is in open conflict with our concepts of classification.

(2) *Subspecies.* Recent discussions, typified by those of Wilson and Brown (1953, SYSTEMATIC ZOOLOGY, Volume 2, page 97) and Voous (1954, *Bulletin of the British Ornithologists Club,* Volume 74, page 25) indicate that there is widespread dissatisfaction with the subspecies concept and its application in zoology. Such dissatisfaction is by no means new, and similar statements can be found in the zoological literature of the last fifty years. A study of such criticism reveals rather clearly that it is directed against either one or both of the following two assumptions: first, that the subspecies is a definable, biological unit; and two, that the subspecies is a category like the species and with the same objectives, but on a lower taxonomic level.

Any attempt to disprove these assumptions should be welcomed. The subspecies is not at all like the species. It is in principle a purely subjective category, even though there are many cases in which there is no difficulty about defining a given subspecies. The subspecies is merely a strictly utilitarian classificatory device for the pigeonholing of population samples. I believe that the definition adopted by Mayr, Linsley, and Usinger (1953, page 30) makes this perfectly clear: "Subspecies are geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of the species." No one will deny that there are awkward and insoluble situations, such as clinal series of subspecies or such as polytopic subspecies.

The real question is whether such difficulties should induce us to eliminate the category subspecies altogether, as suggested by Wilson and Brown. Personally I feel that this would be a mistake because the criticism raised against subspecies is valid for any taxon which is composed of groups of subordinate taxa (such as the subspecies is of local populations). Should we, for instance, throw out the genus, because admittedly we now recognize polyphyletic genera in many groups of animals? Should we get rid of the genus because many genera are ill-defined and grade almost insensibly into neighboring genera?

Suppose we would eliminate the category of subspecies, what could we have in its place? Two alternate suggestions have been made. The first one is to replace it by clines. This indeed works fairly well where a series of populations has an essentially longitudinal distribution, as for instance along a coast, along a river, or along a mountain range. But clines are often quite ill-defined on broad expanses of continents, and in such situations there is usually a different cline for every character. For instance, among Australian birds there is nearly always a south-north cline of diminishing size, obeying Bergmann's rule, and a concentric cline from the humid outer periphery of Australia toward the arid interior. The latter cline is one of diminishing intensity of coloration (paling) obeying Gloger's rule. Now which of the two clines shall we use in our classification? Even more difficult is the situation where populations have an insular distribution. Insular populations show well-defined clines only very rarely.

The alternate proposal is to refer to population samples of a species merely by the binomen and the locality. This procedure apparently assumes that samples from different localities are equally different from each other and that a system of locality designation is sufficient to convey a maximum of information. Actually this is not at all the case. Quantitative data are not available, but my impression, based on a study of many hundreds of continental

and insular species, is that smooth clines are far less frequent than situations where there are rather well-defined subspecies borders. Furthermore, even in the case of isolated populations, locality designation is not necessarily very revealing. For some are so similar to each other as to be profitably included under one subspecies name while others are conspicuously different. Designation by locality utterly fails to bring out such degrees of difference.

My conclusion then is that the modern critics of the category subspecies are quite right in insisting on the subjective nature of subspecies and in criticizing the excessive splitting of continuous, clinal chains of populations, but that attempts to eliminate the subspecies category altogether are by no means an improvement on the situation. Indeed it can be predicted that the adoption of this proposal would rapidly lead to a breaking up of most currently accepted polytypic species by raising the better-defined isolated subspecies to the rank of full species, as indeed has been suggested by one of these critics.

(3) *Super- and sub-taxa on the family and ordinal level.* The Copenhagen Congress adopted a number of provisions concerning authorship, date, and type of the various categories on the level of family and order. It was realized at the time of their adoption that some of the new provisions might raise problems that had not been fully explored. This was particularly true for the recommendation incorporated in paragraph 46 (and 66, section 2) of the "Copenhagen Decisions." It is my opinion that this recommendation oversimplifies the situation and is in conflict, at least in one of the possible applications, with the basic principle of the type method as well as with the stability principle of the preamble of the rules.

Paragraph 46 decrees that names in the family group of categories shall be "coordinate with one another." Stated simply this means that a name proposed for a taxon in any category of the family group of names shall date from its original date of publication, when subsequently applied to a higher or lower category. Thus a name given to a subfamily or a superfamily shall date for the purposes of priority from the date on which it was first proposed (regardless of termination) for any category in the family group of names. At first sight this seems an eminently reasonable proposal. Closer analysis however shows that there are complications. These will appear from a discussion of the possible applications of paragraph 46:

(A) *Proposing a "sub-taxon."* This causes no difficulties. Any author who proposes a new family designates a type genus (by direct citation or indirectly by choice of the family name). He thereby implicitly designates the type genus of the nominate subfamily (and nominate tribe). These nominate sub-taxa are zoologically determined by their type genus and such nominate sub-taxa should therefore date from the publication of the name of the original taxon, even if the sub-taxon was not formally proposed at that time. This principle has long been universally adopted on the level of genus and species for date and authorship of the nominate subgenus and the nominate subspecies. So far as I can determine, it does not violate any general principle of classification or nomenclature. Application of paragraph 46 to sub-taxa on the family level (and of paragraph 66, 2 to sub-taxa on the ordinal level) then seems reasonable and legitimate.

(B) *Proposing a "super-taxon."* There are at least two very different ways of proposing a super-taxon. They are different from the zoological point of view and from the nomenclatural point of view.

(*a*) By raising a subordinate taxon to a higher rank. Raising the rank of a taxon does not change its zoological contents. It merely changes its relation to other taxa. The unit itself remains the same when, for instance, I propose to raise a family to the rank of a superfamily. There is no reason or excuse for changing the type of

the new superfamily, and again, as in (A) above, application of paragraph 46 seems reasonable and legitimate. This applies equally to the raising of a tribe to the rank of a subfamily, that of a subfamily to the rank of a family, and of a family to the rank of a superfamily. In all these cases, the original concept of the zoological group will be retained (with the possible addition or subtraction of a few genera), the only change being that of ranking. Application of the provisions of paragraph 46 should be rigidly construed.

(*b*) By combining several previously unconnected taxa into a new super-taxon. If an author combines a number of families into a new superfamily, he proposes a brand-new zoological unit. This is not a nomenclatural but a taxonomic activity. In view of the provision of the preamble of the Rules, adopted in Copenhagen, which in turn spells out what has been the acknowledged application of the Rules ever since they have been proposed, no rule should interfere with the taxonomic freedom of an author. An author who proposes a new higher category (not merely raising a lower one in rank) has the privilege and the duty of selecting the central unit that should serve as the "type" of the new unit. This is axiomatic in the whole type method which through the years has become such an important cornerstone of the rules of nomenclature. On the generic level this right of the author is fully acknowledged in the rule which states that the author of a tribal name, subfamily name, or family name can select any included genus as the type, not necessarily the oldest one. I maintain that the same situation applies on higher levels where an entirely new zoological grouping is proposed.

There has been at Copenhagen some awareness of this problem, and exceptions to the rigid application of the priority principle to the lumping of families were granted in paragraph 45. These provisions appear to be sufficient for all probable exigencies at the family level.

The situation is more serious with respect to superfamilies (and by analogy with respect to superorders). I propose that only the names of those super-taxa should be coordinate which are due to raising of rank of a pre-existing taxon. In all cases where the proposal of a new super-taxon is the proposal of a new zoological classification, the author of the new super-taxon should have the freedom of type selection regardless of the accidental date of the included families.

This proposal may appear arbitrary at first sight and not in harmony with various previously accepted rules. Actually, however, it seems to me that it merely expresses some of the most important general and specific principles embodied in the rules of zoological nomenclature. It confirms the principle that type selection is an obligation and privilege of the author of a new taxonomic category. It also confirms the principle that nomenclature should not interfere with taxonomic freedom. Finally it is in line with the principle of stability of nomenclature since in the past many superfamilies were proposed without regard to the priority of the included family names, and to introduce at this late date an enforcement of priority would lead to an upsetting of many well-established names of superfamilies. This I think should be avoided, not only for the sake of stability but also because the application of paragraph 46 to superfamilies is, I feel, in direct violation of the above-mentioned basic principles of nomenclature.

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Nomenclatorial Treatment of Specific and Infraspecific Categories

The concern which has been expressed in recent years by many zoologists regarding the overburdening of the nomenclature by the formal naming of great numbers of subspecies, varieties, etc., has resulted in several proposals to remedy or relieve the problem. Some of these suggest the abandonment of formal recognition of some or of all of these names. It has been suggested that such names not be Latinized, that the laws of priority not apply to them, and that authors not be given credit (actually, held responsible) for these names. I believe that none of these proposals provides satisfactory relief, and offer another possibility for consideration by systematists.

To a zoologist who is primarily concerned with the taxonomy of species or with other problems which deal exclusively with species, the naming of numerous infraspecific categories may seem superfluous and often actually puts a great library burden on him. He must deal with long lists of names in his specific synonomies which actually have no bearing on his work; that these categories actually exist is of small concern to him. But to other students infraspecific variation is of great interest, and they believe its study may solve many problems in biology.

In dealing with large numbers of separate entities, it is necessary to attach names to each unit, and rules must be set up and followed in order to arrive at a stable nomenclature. To say that little is gained by naming infraspecific units is to say that little is to be gained by their study. This view may be held by some systematists, but surely not by the majority. Whether infraspecific names should be formally Latinized is relatively unimportant, but to abandon rules in regard to validity of these names would lead to as much confusion as it would in the higher categories of genus and species. We would soon have different authors using different names for a single entity and often the same name for different entities. In regard to giving the original describer credit (or responsibility) for the name, Mayr, Linsley, and Usinger (1953, p. 235) have dealt with the problem adequately and their conclusions are just as applicable for lower as for higher categories. They point out that the author's name is very useful and often absolutely necessary in systematic work. To me it seems, for the above reasons, that abandonment of a formal nomenclature, governed by established rules for all or for any of the infraspecific categories, would only lead to great confusion.

Of all the higher and lower categories used in the classification of animals, with the exception of species, none can be defined unambiguously except as a "division of a higher category and as a group of lower ones." The one category which is recognized as a real unit of nature and has been reasonably well defined is that of species. Most zoologists are in reasonably close agreement as to what a species actually is. Agreement as to the nature of infraspecific categories and the terminology to be used in connection with them has not yet been reached and probably will not be reached until many more careful studies of the problems involved are made. Many zoologists are not interested in these particular problems, but are constantly forced to recognize the existence of names for these subspecies, variations, forms, etc. The main reason for this is that our present rules of priority, etc., treat the species names with the same value or rank as the names proposed for lower categories. They are considered coordinate. We all recognize that the concepts "genus," "species," and "subspecies" are of separate rank zoologically and we treat the concepts of "genus" and "species" nomenclatorially in different ways; we govern selection of names for these groups by different rules. However, in dealing with "species" and "subspecies,"

our rules treat both as if they were the same.

I wish to suggest that because the category of "species" is of different rank from the infraspecific categories, it be so treated nomenclatorially. In other words, only valid names *proposed originally as specific names* should have validity at the level of species. Names proposed by their original author as subspecific, varietal, or other lower-category names should have no standing at a higher level any more than a specific name has standing at the generic level. Similarly, names proposed as species should have no validity at a lower level.

The adoption of such a rule would have several advantages over the present system. Primarily, the studies of species and the studies of infraspecific variation are two separate problems; the interchangeability of names between the groups only complicates their study. Another advantage would be that a zoologist would have to deal with fewer names when studying any one category. Check lists and monographs could be of species only, if so desired, and legally completely ignore lower categories with no danger of overlooking a possible synonym or homonym at another level. If a student disapproved of subspecies, he could quietly ignore them; we would have more peace in the family.

The acceptance of such a rule would undoubtedly present a number of problems which would have to be worked out before its adoption. One problem would be that many specific names now in use were originally proposed as subspecific names and so would seem to be no longer available. However, they would be available if an exception were made for the period before the adoption of the rule, stating that such names had been validated by their later use at the species level. This exception would be made to apply only for the period before the adoption of the rule. It would mean that all such subspecific names which had ever been validly elevated to specific rank would have to be retained in the specific synonomy; but, even so, the vast majority of subspecific names could be legally dropped from our lists of species. In this way, no changes in present nomenclature would be necessary. Any other problems of this nature could possibly be dealt with in a similar manner.

The adoption of the above rule would affect mostly specific names. A similar set of rules would have to be adopted to govern names proposed for lower categories. I feel that subspecific names could then be freed of attachment to generic names and attached only to specific names where they properly belong, thus simplifying the handling of them. This suggestion would not solve most of the problems of lower-level names, but should, if adopted, simplify our nomenclatorial procedure concerning the one category which most zoologists have occasion to refer to the most often: the species.

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Further Thoughts on Subspecies and Trinomials

To one who, as a systematist, has felt himself increasingly overwhelmed by the advocates of trinomial nomenclature, the article by Wilson and Brown (1953) comes as a refreshing relief. The present author has been trying to live with the trinomial system for years, but the attempt has only resulted in the increasing realization of its disadvantages. Some of these will be discussed here by way of supplement to Wilson and Brown's paper. At the outset it should be emphatically stated that the present author has no quarrel whatever with the subspecies as a zoological concept. His objections are entirely directed against the associated subject of trinomial nomenclature. However, the fact that the two matters in the past have been inextricably intertwined makes it difficult to separate them at this date.

As Rensch (1934) has so ably shown, the adoption of trinomial nomenclature has been instrumental in demonstrating the tremendous part that geography plays in speciation and in bringing order to the chaos that formerly existed in the systematic treatment of allopatric forms. For these advances all systematists owe a debt of gratitude to the trinomial system. Unfortunately the adoption of this system has also left us with a legacy, the implications of which seem to be generally overlooked. Since, according to the present Rules of Zoological Nomenclature, no properly formed trinomial can be validly ignored, and since (as Wilson and Brown point out) there is almost no lower limit to the size of the unit to which a new subspecific name can be validly applied, the multiplication of nomenclatorial problems for future generations seems infinite. One suspects that under the present Rules the future systematist will be something of an intergrade between a philologist and an attorney. Whether, as such, he will have any time for zoological work and whether he will be of any use to society appear highly questionable. Indeed, it seems more probable that if present conditions continue the future systematist will be the butt of a zoological profession that pays no attention to anything he may do. At this point the taxonomist's reason for existence will have terminated.

But to return to the present, there are today three main categories of people who come into contact with trinomial nomenclature: amateur naturalists, zoologists in non-taxonomic fields, and systematists. The relationship between trinomial nomenclature and each of these groups will be briefly discussed. Those who write handbooks are probably most acutely aware of the impact which the trinomial system has on the amateur. Peterson, after considering trinomials in the text of the earlier editions of his *Field Guide to the Birds* removes them to an appendix in the 1947 edition. He explains his reasons for doing so at some length (1947, pp. 256-257) and concludes that subspecies "should not concern the field amateur."

As to the non-taxonomic zoologists, it has been my experience with various zoology departments that such men have little benevolence toward zoological nomenclature of any sort. Binomial nomenclature, they will usually grant, is a necessary evil, but to them trinomial nomenclature is an unnecessary one. Two explanations for the existence of trinomials have at one time or another been (jokingly?) suggested to me by zoology department colleagues. One is that the subspecies was thought up in order to have something to name in those groups where all the species had already been described. The other suggestion gives entire credit for the trinomial system to ornithologists. It states that ornithologists, having examined the bills, feet, and feathers of all of their species, invented the subspecies in order to stall off the day when they would have to investigate some other characters. There is unfortunately an element of truth, and also unfortunately of bitterness, in both these assertions.

With regard to systematists, it is they who have sired the trinomial system, and one would therefore expect it to be of particular benefit to them. Yet there are two cogent reasons for thinking that even today, let alone in the future, trinomial nomenclature is more of a hindrance than a help to them. One, the increased part of the taxonomist's time that must be devoted to nomenclatorial considerations, has already been discussed.

The other is that the trinomial system may on the whole obscure an understanding of infraspecific relationships. It is indisputable that many species break up into more or less typical geographic subspecies and that the trinomial system is and has been of value in bringing these to attention. Nevertheless even with these the important point is the genetic (and hence morphological) continuity between them whereas trinomial nomenclature is almost exclusively concerned with their differences: it is the intergrades between two morphologically different forms that constitutes the critical evidence for subspecies, yet it is these same intergrades that are left unnamed and hence unemphasized under the trinomial system.

There are, however, other types of variant infraspecific populations besides subspecies. Clines and ecotypes are examples. But since subspecies in practice are based on sample differences, and since similar sample differences also occur in other types of infraspecific variation, all sorts of variant populations have been named as subspecies. This has two results. First, the phenomena assembled under the name of subspecies are so heterogeneous that the subspecies concept has lost nearly all meaning. It is no wonder therefore that widely divergent views are held among systematists themselves concerning the nature of the zoological entity that the subspecies represents (cf. Dice, 1940, and Mayr, 1942) and that non-taxonomists are utterly confused by it. Second, the fact that other types of infraspecific population variation besides geographical subspecies do frequently occur has been largely lost from view by systematists. For example, taxonomists neglect the cline as a phenomenon in itself in their efforts to resolve the insoluble riddle of how many subspecies should be recognized within the cline.

Indeed, the idea has developed that any populations differentiable under the "75% rule" (or some variant of it) are subspecies, and an attempt is then made to discover a zoological entity that coincides with the trinomial unit thus differentiated. There is none. So long as infraspecific units are defined on the basis of population differences rather than continuities these units must remain artificial. They will be not only heterogeneous but often polyphyletic. That the systematist, theoretically trying to interpret genetic relationships, should come to recognize and name polyphyletic units, as is done today in subspecies (Mayr, Linsley, and Usinger, 1953, p. 32), seems highly peculiar.

The whole preceding section may be summarized by stating that in this writer's opinion trinomial nomenclature is leading systematists into a costly diversion of effort which is, at best, of dubious value.

The best solution to the dilemma would seem to be to remove all infraspecific categories from any validity under the Rules of Zoological Nomenclature. This would not only relieve systematists of numerous hours lost among nomenclatorial morasses but it would free the study of infraspecific categories from the strait jacket now imposed by the "75% rule" (and other artificial criteria). Such a solution would also relieve the systematist of some of the animus now held toward him by those outside his profession.

Trinomial nomenclature is merely an afterthought to the Linnaean system. Presumably it could be subtracted from binomial nomenclature with no more difficulty than that with which it was originally added. The removal of trinomials from nomenclatorial validity might be effected in two ways. One, suggested by Wilson and Brown (1953, p. 108), is that after a certain time newly named

subspecies should have no status under the Rules. The second is that all subspecies names be retroactively removed from nomenclatorial validity in the same way and by the same method as infrasubspecific names have already been dealt with (*Bull. Zool. Nomencl., 4:* 93-95, 1948). Even if the latter, more radical but possibly more easily executed, method of elimination were undertaken, I can see no reason why many of the present suitable subspecific names should not be used (except that they would not have nomenclatorial status, types, or italicized names). In this way the advantageous features of our present infraspecific edifice could be retained, but the more deleterious sections discarded and, where necessary, rebuilt on other bases and along other lines.

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On the Nature of Species in the U.S.S.R.

(*Concluded from p. 68*)

very much like the kind of spontaneous generation which Spallanzani refuted as far back as 1775. It is impossible to tell from his writings whether Lysenko realizes all this. But it is revolting to see numerous competent biologists in the U.S.S.R. being forced to pay at least lip service to "Michurinist Biology" in their publications.

The recent news that Lysenko is falling into disfavor in the U.S.S.R. makes appropriate a re-examination of his views on the nature of species and their formation. This paper by **THEODOSIUS DOBZHANSKY**, Professor of Zoology at Columbia University, provides the essence of Lysenkoism for comparison with those widely accepted concepts which are carefully evaluated in the preceding article by Meglitsch. Professor Dobzhansky's article originally appeared in the *Journal of Heredity* (1953, *44*:20–22) under the title "Lysenko Progresses Backwards" and is reprinted without change with the kind permission of the author and editor.

People and Projects

Two distinguished members of the Society of Systematic Zoology have been honored by the National Academy of Sciences; Professor Alexander Petrunkevitch and Professor Ernst Mayr were elected to membership at the last meeting.

Their election increases the list of Academy members primarily interested in systematic zoology to seven: Hubbs, Kellogg, Mayr, Petrunkevitch, Romer, Simpson, and Wetmore; approximately 13 per cent of the membership in the Section on Zoology and Comparative Anatomy.

Also noteworthy was the presentation of the Daniel Giraud Elliot Medal to Raymond Carroll Osborn for his monograph on the Bryozoa of the Pacific Coast.

James A. Peters, of the Department of Biology, Brown University, has received a grant from the American Philosophical Society that will enable him to spend three months, from June to September, in Ecuador, continuing his studies of the herpetology of that country. Present plans are to spend a month each in the Amazon lowlands, the inter-Andean plateau, and the Pacific slope. He will be accompanied by his wife, Dorothy Beane Peters.

By a recent action of the Tennessee State Board of Education, East Tennessee State College, at Johnson City, has been approved to offer a graduate major in biology, leading to the Master of Arts degree. Course work and research will be offered in invertebrate morphology and systematics, under the direction of Perry G. Holt (Ph.D., University of Virginia).

Students and teachers of marine zoology on the West Coast are fortunate to have such a complete guidebook to their intertidal life as is provided by *Intertidal Invertebrates of the Central California Coast:* S. F. Light's *Laboratory and Field Text in Invertebrate Zoology,* revised by R. I. Smith, F. A. Pitelka, D. P. Abbott, F. M. Weesner, with many other contributors. (Univ. of California Press, Berkeley 4, Calif., 1954. $5.00.) This book contains complete and, in many instances, original keys to the intertidal invertebrates as well as to the algae and flowering plants and the fishes living in the same habitats. This guide will unquestionably be most useful for study along the central California coast but undoubtedly can be used with profit anywhere along the western coast of the United States.

Dr. Benno Kummer, who has studied the development of the skull in the human and in several anthropoids by using Thompsonian coordinate grids, finds no confirmation of the hypothesis that the evolution of man has involved "fetalization." His interesting analyses are published under the title of "Untersuchungen über die Entwicklung der Schädelform des Menschen und einiger Anthropoiden," in the series *Abhandlungen zur Exakten Biologie;* 44 pages; 9 marks (German).

In "The Fresh Water Fishes of Nova Scotia" (*Proc. Nova Scotian Institute of Science,* vol. 23, pt. 1, 1950–51) D. A. Livingstone gives detailed information on the occurrence of the 33 species of fishes which have been found in the fresh waters of this province. The distribution pattern of the 12 strictly freshwater species indicates that they have entered Nova Scotia by way of the Isthmus of Chignecto since the recession of the last ice sheet.

The close interdependence of ecology and taxonomy, evident to all systematists, is especially clear where intensive study

is in its early stages, as it is in the East Africa lake region. The Annual Report for 1952 of the East African Fisheries Research Organization provides a fascinating summary of the work done at the Organization's laboratory at Jinja, Uganda, on the north shore of Lake Victoria. Although some of the most interesting parts of the report deal with studies on the natural history of fishes living in the lake and neighboring swamps, the work of the laboratory is by no means restricted to fish biology. The hydrology of the lake and swamps, the algae, aquatic insects, molluscs and the parasites they share with man, crocodiles, and fish-eating birds are all reported upon, providing some concept of the breadth and scope of the laboratory's activities. The recent findings on *Tilapia* and *Haplochromis* will be of interest to anyone concerned with the puzzles which the species flocks of these cichlid fish provide.

Readers of SYSTEMATIC ZOOLOGY will remember H. J. Van Cleave's article on evolution in the Acanthocephala. In a posthumously published monograph, "Acanthocephala of North American Mammals" (*Illinois Biol. Monog., 23,* Nos. 1, 2), Van Cleave had begun to integrate the results of a study which lasted a lifetime. Several other monographs were planned to complete this integration. The published volume, 179 pages in length, covers the methods of preparing material, provides keys to the classes and orders of Acanthocephala and to the families and genera, as well as to many of the species known to parasitic mammals. Of more general interest are the sections dealing with the correlations between habitat and taxonomy, and the many problems relating to the geographical distribution of these parasites. List price, $5.00 cloth, $4.00 paper, from the Univ. of Illinois Press, Urbana.

A new serial publication, *Tulane Studies in Zoology,* will be devoted primarily to the zoology of the Gulf of Mexico and bordering regions. It was initiated to fill a long-felt need to encourage and facilitate the publication of papers concerned with the zoology of this region, especially those too long for other journals. Contributors need not be members of the Tulane University faculty.

Each paper is issued as a separate number and may be purchased separately by individuals, but no subscriptions are accepted. This periodical is to be distributed almost entirely in exchange for other biological publications. Communications from exchange librarians will be welcomed by the editor, G. H. Penn, Department of Zoology, Tulane University of Louisiana, New Orleans, La., U. S. A.

The following papers have been accepted for publication in the first volume: "A contribution on the life history of the lizard *Scincella laterale* (Say)," by Richard M. Johnson (app. 12 pages); "An outline for the study of a reptile life history," by Fred R. Cagle (app. 24 pages); "A population of Holbrook's salamander, *Eurycea longicauda guttolineata* (Holbrook)," by Robert E. Gordon (app. 8 pages); "A new burrowing crawfish of the genus *Procambarus* from Louisiana and Mississippi," by George H. Penn (app. 8 pages); "A redescription of the crawfish *Procambarus hinei* (Ortmann)," by George H. Penn (app. 8 pages); "The life history of the crawfish *Orconectes* (*Faxonella*) *Clypeatus* (Hay)," by Elsie W. Smith (app. 16 pages); "The taxonomic status of the mid-Gulf *Amphiuma,*" by Imogene R. Hill (app. 16 pages).

In a paper entitled "The History of Keys and Phylogenetic Trees in Systematic Biology" (*J. Sci. Lab. Denison Univ., 43,* Art. 1, pp. 1–25), E. G. Voss has presented a fund of interesting information on systematic arrangements specifically designed to aid in the identification of organisms, and diagrams intended to indicate the relationships of major groups. He has included many facsimile reproductions of keys and trees of importance in the historical development of both botany and zoology.

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.